PROTEIN GROWTH IN PIGS

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ABSTRACT OF THESIS

The following aspects of protein growth in pigs were examined:

I. Shape of daily protein and lean deposition rate against age and live weight. 45 Large White pigs were fed to appetite; littermate trios were serially slaughtered between 55 and 330 days of age. Daily feed intakes increased linearly until 140 days and 85 kg LW. Daily protein and lean gains, 55-195 days and 20-150 kg, were 0.128, 0.255 (boars), 0.108, 0.221 (gilts), 0.117, 0.234 (castrates). Dissected lean was 2.21 total body protein. Estimated ME_M value, 0.545 MJ ME per kg $W^{0.75}$ d^{-1}; k_p was 0.27 and k_l, 0.73.

II. Body composition after weaning. Weight stasis concealed substantial lipid loss from carcass fatty tissue and continued growth of carcass muscle plus bone. Recovery from post-weaning growth check was more rapid when diets of high nutrient density were offered. Thirty-five female pigs were given 4 intake treatments and serially slaughtered between 25 and 70 days. During refeeding previously-restricted pigs gained 75.4 g protein d^{-1}; appetite-fed controls gained 67.4 g d^{-1}. Refed pigs did not consume more food, or deposit protein more rapidly, than controls of the same age or body weight. Twenty-eight pairs of entire male pigs were grown from 5.6 to 25 kg on two diets of differing ingredient composition and nutrient density. There were no differences in carcass composition at 25 kg or daily feed intake (0.81 vs 0.76 kg). Pigs fed the diet of higher ingredient quality and nutrient density reached 25 kg fourteen days sooner and ate 8.9 kg less in total. Post-weaning growth was constrained by the poorer quality diet.

III. Compensatory nitrogen retention. Seventy-one Large White barrows were fed various sequences of dietary nitrogen intakes over 30 days. Following nitrogen deprivation, compensating animals retained 2.7 (Trial 1) and 4.2 (Trial 2) g N d^{-1} more than controls. Evidence suggests extra nitrogen to be used to replenish labile nitrogen stores depleted during nitrogen deprivation.

DECLARATION

This thesis has been compiled by myself and embodies results from my own research investigations.

Jane Bronwyn Tullis

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GENERAL INTRODUCTION

Interest in protein growth and its characteristics is fundamental to pig production: protein, by its contribution to carcass lean, represents the commercially valuable body component. Deposition of protein and lean at less than potential rate detracts from the efficient employment of inputs such as pigs, feed, housing and labour.

In the first of three Sections, potential daily protein and lean gains are assessed by the technique of serial slaughter. Carcass dissection and chemical analysis of dissected fractions are used to identify the destination of protein deposited in the empty body. To evaulate the various influences on protein and lean gains exerted by age, live weight, sex, genotype and appetite, pigs were grown over a wide range in age (14 to 332 days) and live weight (5 to 200 kg), pigs of three sexes (boar, gilt and castrate) were selected from different litters (to introduce an element of genetic variation) and were at all times permitted to express their appetite potential.

The second Section investigates the repercussions of weaning for body composition in young pigs, notably with regard to the priority afforded to protein growth during weight stasis induced by intake depression. Once again, serial slaughter is used to distinguish compositional changes, and in one study, carcass dissection provides information regarding tissue changes within dissected fractions. Capacity for recovery of protein growth forgone during a growth check is explored using young pigs, including the monitoring of voluntary feed intakes during refeeding and examination of associated tissue gains. Two experiments are described which seek to clarify the intake and growth response of young pigs to diets of different nutrient density offered subsequent to weaning.

Section III is concerned with the phenomenon of compensatory nitrogen retention. Conventional nitrogen balance techniques are used to quantify nitrogen retention during periods of nitrogen deprivation and refeeding. Semi-synthetic diets of differing nitrogen content were fed in a number of combinations to produce different sequences of nitrogen intake. Response to higher nitrogen intake following a period of low nitrogen intake was measured in the short- and longer-term to test the existence and persistence of a compensatory mechanism.

Results obtained from these studies should allow a number of conclusions to be drawn regarding the inherent limits to daily protein and lean deposition and the flexibility of protein growth under a range of nutritional circumstances.

SECTION I

Quantification of daily protein and lean deposition rate in entire male, female and castrated male pigs fed to appetite

INTRODUCTION

Growth, the quantitative increase in body mass and body component mass over time, was investigated in pigs by the Cambridge School and summarized by Pálsson (1955).

A strict relationship was established between dissectible muscle and body weight, imputing that the sigmoidal pattern of increase in the latter with age was mirrored by sigmoidal increase over time of lean and, by implication, protein. The characteristics of this growth curve are therefore those of exponential increment in lean and protein mass in early life followed by curvilinear increase for lean and protein as maturity is approached; a point of inflection occurs at the juncture of these two phases. However, this form of growth curve also allows the interpretation that increase in lean or protein mass does not depart radically from linear over a substantial section of its progress. Thus, on a day-to-day basis, daily lean and protein gains would be virtually constant. Contradicting this interpretation of protein and lean growth is the proposal of a quadratic form to daily protein and lean deposition, featuring a distinct peak to daily gain, and one which is sustained over a very narrow range of age or live weight (Hammond, 1933; Clausen, 1953). These two hypotheses are illustrated in Figure 1.1. The thick horizontal line represents the concept of a fixed ceiling to daily protein deposition rate, applicable over a large section of active growth; the broken curve represents the idea of a peak in daily protein deposition rate at around 70 kg live weight, with both smaller and heavier animals being of lower protein growth potential. Thorbek (1975) collated nitrogen retention$_{L}^{(NR)}$ data from nineteen experiments in which feed intakes by castrated male pigs were considered sufficient to support maximum daily protein deposition. Mean values

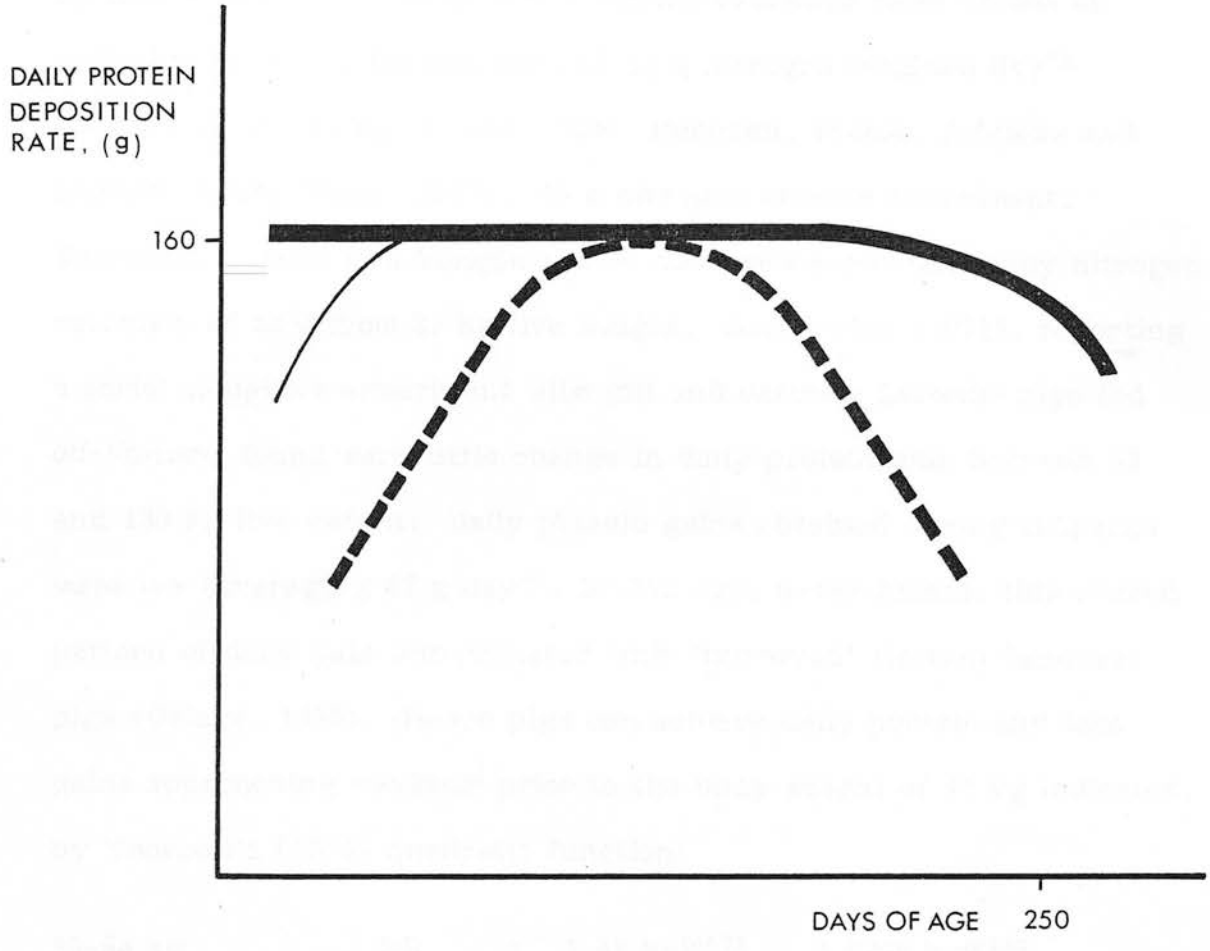


FIGURE 1.1: Two hypotheses for the pattern of daily protein deposition rate (g) relative to age. (See text for explanation.)

from these trials trace an increase in nitrogen retained per day from 10 g at 5-10 kg live weight, to 15 g at 20-30 kg, reaching a peak of 20 g over the period 60 to 80 kg, and starting to decline from 90-100 kg live weight. Individual measurements exceeded mean values at lower live weights, for example, 17-19 g nitrogen retained day^{-1} between 20 and 30 kg (Evans, 1958; Hencken, Freese, Addicks and Lenkeit, 1963; Wenk, 1973). In a nitrogen balance experiment, Sundstøl, Standal and Vangen (1979) observed a constant daily nitrogen retention of 22 g from 35 kg live weight. Doornenbal (1971), reporting a serial slaughter experiment with gilt and castrate Lacombe pigs fed *ad-libitum*, found very little change in daily protein gain between 50 and 130 kg live weight; daily protein gains obtained during this trial were low (averaging 67 g day^{-1}, 50-130 kg), nevertheless, this overall pattern of daily gain was repeated with "improved" German Landrace pigs (Oslage, 1965). Hence pigs can achieve daily protein and lean gains approaching maximum prior to the body weight of 84 kg indicated by Thorbek's (1975) quadratic function:

20-84 kg live weight	NR ($g\ day^{-1}$)	=	$1.48\ kgW^{0.75}$ (±0.023)	- $0.0266\ kgW^{1.50}$ (±0.0011)

Furthermore, the goodness-of-fit of this function to nitrogen retention data places considerable weighting on a few measurements of daily nitrogen retention in heavier pigs, 150 to 170 kg live weight: 12 g NR day^{-1}, non-pregnant gilts (Elsley, Anderson, McDonald, MacPherson and Smart, 1966) and 14 g NR day^{-1}, castrated males (Oslage, Fliegel, Farries and Richter, 1966). These values may have suggested a more precipitate rate of decline in daily protein gain from peak gains than occurs in practice. Differentiation of the sigmoidal growth of lean and protein masses over time suggests a 'skewed' quadratic shape to daily

gains, resulting from a far steeper increase in rate of gain by young pigs than rate of decline in daily gain by heavier pigs approaching maturity.

Miller and Payne (1963) declared nitrogen retention in growing pigs to be a function of protein intake, protein quality and energy intake, evidence to corroborate this theory being largely confined to younger pigs (Lassota, 1960). Conversely, Møllgaard (1955) interpreted nitrogen balance results from pigs between the ages of 60 and 200 days to attest the existence of a maximum ceiling for nitrogen retention related to pig age. These two theories were combined by Kielanowski (1972) to form the hypothesis that young pigs of high protein growth potential are prevented from realising their potential daily protein gain by feed intake constraint:

> *".. until a certain plateau is reached, nitrogen balance depends strictly on the amount and quality of protein in the ration, and pigs in which the protein deposition is restricted by nutritional factors will behave as those in which the genotype sets the limit."*

Later in growth phase, pigs are no longer restricted to daily protein gains commensurate with achieved nutrient intake and can deposit the maximum daily protein and lean gains dictated by their genetic constitution. The fine solid line in Figure 1.1 represents the improved daily rate of protein deposition by young pigs which have been persuaded to consume more food.

Genetic potential for protein and lean deposition is one of two endogenous factors controlling rate of gain, the other being sex of pig. Thorbek (1975) noted a 3-5 g day^{-1} between-pig variation in nitrogen retention and suggested that individual pigs adhered to the

same basic pattern of daily nitrogen gain but differed genetically in the absolute magnitude of their gain. Analysis of data from Danish Progeny Testing Stations by Kielanowski (1966) revealed a 0.18 increase in daily protein gain produced by 30 years of selection (77 to 93 g day^{-1}). It is anticipated that selection for higher daily rates of protein deposition will favour later-maturing strains of pig with higher protein and lean masses at maturity (Webster, 1980). Endocrine status is implicated in genetic potential for protein and lean accretion. Thyroid hormones appear to alter growth rates of muscle by regulating protein degradation rate as well as synthetic rate (Brown and Millward, 1980); rats with greater protein growth rates showed reduced protein degradation per unit of protein synthesis (Bates and Millward, 1981).

Sex of pig influences maxima for daily protein and lean deposition, with females ranking below entire males and above castrated males (Piatkowski and Jung, 1966; Fuller, Gordon and Aitken, 1980).

Factors external to the animal which will affect protein and lean growth rates include diet composition (coupled with feed allowance), environmental temperature, disease challenge and housing design (from the viewpoint of social behaviour). Restricted feed intake, or imperfect matching of nutrient supply to nutrient requirements, will reduce daily protein and lean gain (Halter, Wenk and Schürch, 1980). Deposition of protein is largely independent of temperature (Close and Stanier, 1980), except at extremes. While piglets weaned at three weeks of age have a lower critical temperature of 28°C (Le Dividich, Noblet, Aumaitre and Vermorel, 1980), growing pigs' daily protein gains appear uninfluenced by temperature within the range of 14 to 25°C (Fuller, 1964; Sørensen and Moustgaard, 1964). Disease, whether

clinical or sub-clinical, will limit protein gain and increase heat output. Germ-free rats showed reduced protein turnover in the gut, had higher rates of protein deposition and lower heat loss than contemporary rats with normal intestinal flora (Visek, 1978).

Much attention has been focussed on the appropriate combination of dietary protein and energy to promote optimal growth rate, feed conversion efficiency and carcass quality. The most effective and economic of feeding stratagems will be those which match nutrient intake to nutrient requirements for efficient growth; the latter comprises maximum protein accretion and a minimum of fat deposition. Fundamental to such a policy is a knowledge of tissue growth potentials. Calculation of daily protein supply would be hindered by lack of precise information regarding the boundaries to daily protein and lean deposition. A few values have been suggested for maximum daily protein deposition (kg day^{-1}):

Boars	0.130+[1]	0.130[2]	Genetically exceptional	0.130+[1]
Gilts	0.110	0.112	Improved	0.110
Castrates	0.090	0.100	Unimproved	0.080

[1] Kielanowski (1969)

[2] Piatkowski and Jung (1966)

Danish Progeny Testing Station data provide examples of values obtained by comparative slaughter and illustrating genetic variation: 0.075 to 0.125 kg protein day^{-1}, 25 to 90 kg live weight (Clausen, Nørtoft Thomson, Pedersen, Busk and Christensen, 1971). Similarly, genetic variation in pig breeding companies' stock is apparent in values cited in the MLC Commercial Product Evaluation Report (1978) for gilts and castrates fed *ad-libitum*: 0.119 to 0.160 kg protein day^{-1}

(extrapolated from daily lean tissue gains) between 27 and 91 kg live weight. Carr, Boorman and Cole (1977) used data from pig experiments judged to have few dietary or environmental constraints to the attainment of maximum daily nitrogen retention to produce the following relationship between nitrogen retention (NR, g day^{-1} per kg $W^{0.75}$) and body weight (W, kg):

$$NR = 3.324 - \underset{(\pm 0.0051)}{0.098\ W} + \underset{(\pm 0.0001)}{0.001\ Z} \qquad r = 0.96$$

Where Z is equivalent to W^2 for body weights equal to or less than 45 kg and 45 (2W - 45) for body weights of more than 45 kg. This function, incorporating data from Large White and Landrace pigs of three sexes (boar, gilt, castrate), predicts more or less constant daily nitrogen retention between 20 and 90 kg live weight. However, estimated nitrogen retentions at higher live weights (for example, 4.2 g day^{-1} at 150 kg) are well below the measurements detailed earlier (12 and 14 g day^{-1}, Elsley *et al*, 1966; Oslage *et al*, 1966).

The information available concerning protein and lean growth potential is far more abundant for gilts and castrated males than for entire males.

The rest of this Section will describe an experiment designed to quantify daily protein and lean deposition rates by entire male, female and castrated male pigs kept under conditions conducive to the achievement of growth potential. Pigs were fed to appetite throughout (from 14 days of age until slaughter) on diets high in both protein and energy; an excess of the former nutrient might have caused depression in voluntary feed intake, in conjunction with a failure to provide sufficient readily-usable energy for maximisation of daily protein gain.

It was accepted that this feeding strategy would increase the energy cost of maintenance (by additional work of digestion, Kielanowski, 1967) and would also reduce efficiency of conversion of dietary protein to body protein (Davies, Lodge and Lewis, 1965; Blair, Dent, English and Raeburn, 1969). Environmental temperature was maintained within the recommended range relative to body size and pigs were given a generous space allowance, the energy costs of body movements being considered insufficient to impinge on protein deposition (Blaxter, 1962). Animals were slaughtered according to age (55 to 330 days) and their carcasses dissected into component tissues. In addition, chemical analysis was performed on dissected carcass tissues and non-carcass fractions to provide whole body compositions.

MATERIAL AND METHODS

Fifteen litters from Large White x Landrace sows mated to Large White boars were offered an early-weaning diet as a creep feed from 3 days of age. The ingredient and chemical compositions of the early-weaning diet are presented in Table 1.1. Half of the male pigs in each litter were castrated at 7 days. Pigs were removed from the sow on reaching 14 days of age, weighed, and transferred to the upper two tiers of multi-tier cages. Early-weaning diet was offered *ad libitum*. At 21 days of age, six pigs were selected from each litter on the basis of live weight gain in the 7 days following weaning. Two boars, two gilts and two castrates were penned individually in wire-mesh cages fitted with nipple drinkers and troughs designed to minimise spillage. Pigs were fed three times a day at approximately 08.00, 15.00 and 21.00 hours. If the preceding feed had been consumed entirely then pigs were offered an extra 50 to 100 g of diet at the next feed, that is, feeding was 'to appetite' on a challenge-feeding system. Troughs were scraped daily to loosen food adhering to the sides and base. Pigs were weighed every five days. Room temperature was reduced from 27°C (at 14 days) to 24°C (at 55 days).

From 50 days of age and until slaughter, pigs were given the grower diet whose composition is presented alongside that of the early-weaning diet in Table 1.1. The digestible energy and apparently digestible nitrogen contents of the early-weaning diet were measured using conventional balance techniques with nine castrated male pigs of 44.0 kg live weight (Tullis and Whittemore, 1980). Similarly, digestible energy and apparently digestible nitrogen contents of the grower diet were assessed with six castrated male pigs of 45.5 kg live weight.

TABLE 1.1: Ingredient and chemical composition of the early-weaning and grower diets

	Early-weaning diet[1]	Grower diet
Ingredients (g kg^{-1} fresh weight)		
Ground barley	100	300
Ground wheat	100	100
Ground maize	250	250
Soya bean meal	100	100
Fishmeal ('Provimi' 66)	150	150
Whey powder	200	-
Tallow[2]	50	50
Mineral and vitamin mix[3]	50	50
Dry matter (g kg^{-1}) (DM)	910	901
Chemical composition (g kg^{-1} dry matter)		
Nitrogen	36.7	36.7
Ether extract	87.4	88.1
Fibre	28.0	36.2
Ash	93.4	87.3
Gross energy (MJ kg^{-1}DM)	19.4	19.2
Digestible nitrogen[4]	33.3	31.7
Digestible energy[4] (MJ kg^{-1}DM)	15.8	14.3

[1]Also used in experiments on young pigs - Sections 2B and 2C.

[2]'Priplus 45' fully hydrogenated tallow flake, Unichema International, Bebington, UK.

[3]Containing (kg^{-1} mixed diet): 39 g dicalcium phosphate, 6.5 g salt, 20.0 g zinc bacitracin, 2.5 g 'Coopers 10TE' mineral mix.

[4]Determined directly by balance procedures.

At 55 days a trio of pigs from each litter, comprising a boar, gilt and castrate, was transferred to adjacent individual pens in controlled-environment rooms containing six pens per room. Each pen measured 2 x 1 metres and had concrete slatts to the rear of the pen; the gates and sides of the pens were constructed of tubular metal bars set 6 cm apart, allowing the pigs sight, sound and smell of (and to a limited extent physical contact with) other pigs. Pigs were provided with thick plastic lying boards which covered two-thirds of the slatted floor area. Food troughs, attached to the pen gates, were adjustable in height to cater for a wide range of pig sizes and to limit feed wastage. Individual nipple drinkers were situated to one side of the feed troughs. When pen size became inadequate, partitions were removed and the space allowance doubled to 4 square metres.

Room temperature was maintained in the range 18 to 20°C.

Pigs were weighed every 7 days between 55 days and slaughter.

Littermate trios were slaughtered according to the schedule shown in Table 1.2 below.

TABLE 1.2: Slaughter schedule for trios of littermate pigs between the ages of 52 and 332 days

Planned		Actual		
Days of age	No. of trios	Days of age	No. of trios	Litter No.
55	2	52,55	2	1,2
90	2	91	2	3,4
125	4	123,123,124,126	4	5,6,7,8
160	2	163,165	2	9,10
195	1	195	1	11
230	1	231	1	12
280	1	285	1	13
330	2	330,332	2	14,15

Slaughter and dissection procedure

Pigs were weighed before leaving the Pig Unit and slap numbers applied for subsequent carcass identification. At the abattoir, pigs were electrically stunned, the vena cava severed and blood collected in plastic buckets. After weighing, sub-samples of blood were stored in plastic bottles and the remainder discarded. Hair and scurf were removed by mechanical scrapers during the scalding process. The alimentary tract and associated glands were excised from the body and weighed. Contents of the stomach, intestines and bladder were discarded and the empty tract re-weighed. The heart, lungs (plus trachea), liver, genitalia, flare fat, kidneys and spleen were weighed individually before amassing to form the non-carcass (NC) fraction. The fillet (psoas major muscle) was removed from the left-hand-side of the body, weighed and retained for inclusion with carcass dissected lean. The head, feet (minus toenails) and tail were removed, weighed separately and amassed to form the head, feet and tail (HFT) fraction.

Carcasses were split by sawing to the righthand-side of the backbone (viewed dorsally) such that all vertebrae were included with the left carcass side. All carcass sides were weighed. Right carcass sides were later prepared for human or animal consumption, depending on the age and sex of pig.

Left carcass sides were transported, together with the NC and HFT fractions, to the Carcass Evaluation Unit. Prior to dissection, and following thawing, P2 backfat depth measurements (including skin) were taken by insertion of a metal ruler at a point 6.5 cm from the midline at the head of the last rib. Sides were reweighed and divided into the seven joints indicated in Figure 1.2, namely, hand, collar,

rib streak, rump back, rump streak and ham (MLC, 1975). Each joint was weighed before being dissected into lean, intermuscular fat, subcutaneous fat, skin and bone (sub-divided into vertebral and other bone). Dissected tissues from each joint were weighed individually and the details noted on a standard MLC pig dissection record sheet. Cumulated dissected tissues for a carcass side were minced individually, once through a 13 mm plate and twice through a 5 mm plate. Minced material was mixed thoroughly before sub-sampling to 3 x 1 kg samples; one sub-sample was immediately oven-dried to constant weight at 90°C, a second was freeze-dried and milled before submission for chemical analysis, and the third was retained as a spare sample. The NC and HFT fractions were homogenised, sampled and analysed in the same way as dissected tissues.

Chemical analysis for gross energy was by adiabatic bomb calorimetry, for nitrogen by Kjeldahl digestion, and for lipid by use of the equation: Lipid = (GE - 0.1475N)/0.0393 (assuming the energy content of protein and lipid to be 23.5 and 39.3 MJ kg^{-1} respectively, and protein and lipid to be the only energy-containing components of animal tissue, Whittemore, Moffat and Taylor, 1976). The latter condition is not applicable in the case of blood; analysis of the lipid content of blood was by extraction with petroleum according to the method outlined in Fertiliser and Feeding Stuffs Regulations (1960).

Weights of dissected body tissues were obtained for the whole carcass by doubling the weights of dissected lean plus fillet, subcutaneous fat and skin in the left carcass side. Whole carcass bone was calculated by doubling the weight of other bone in the left carcass side and adding the product to the weight of dissected vertebral bone.

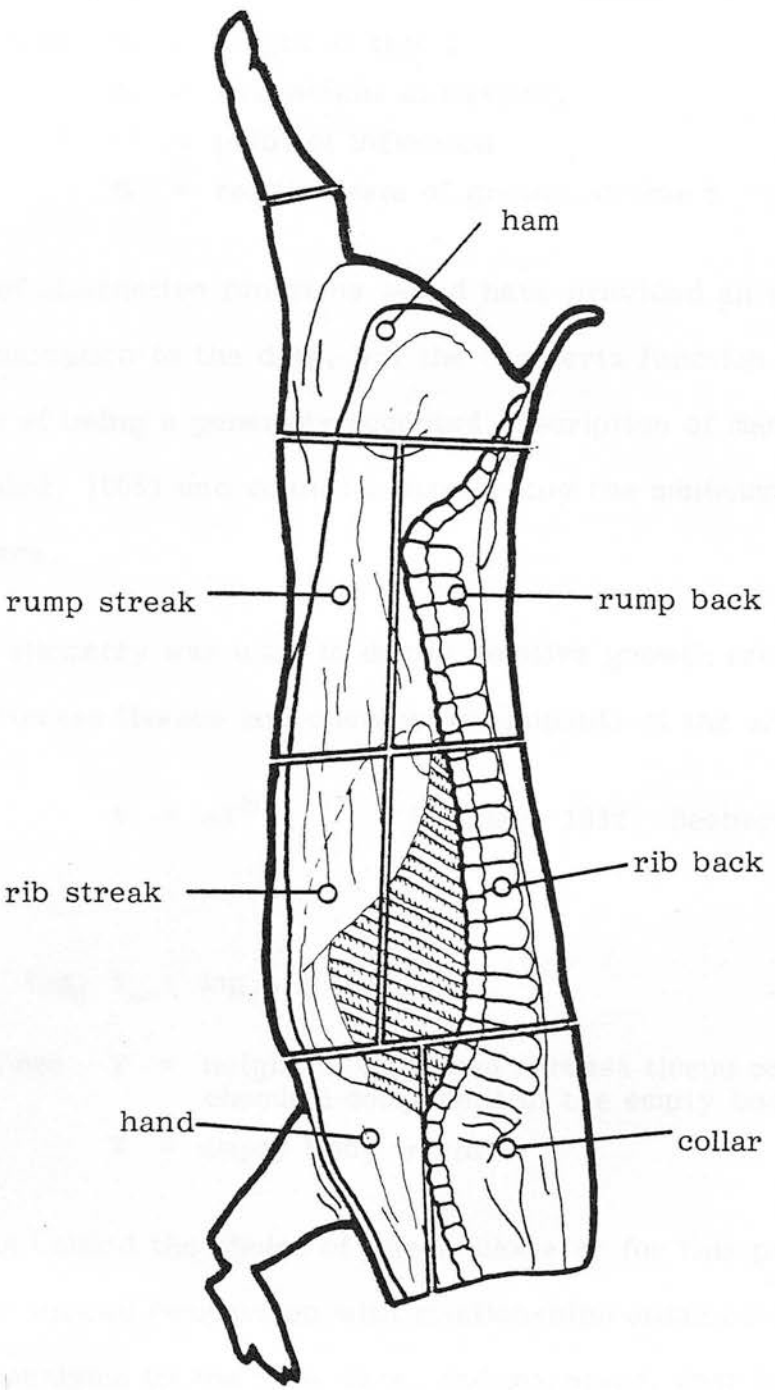


FIGURE 1.2: Standardised joints used in carcass dissection (Meat and Livestock Commission, 1975).

Statistical analysis of data

Change in live weight over time was described for the six pigs in the final slaughter group by application of the Gompertz function:

$$W_t = A.e^{-e^{-B(t-t^*)}} \qquad \text{(Gompertz, 1825)}$$

where W_t = weight at time t
A = live weight at maturity
t^* = point of inflection
B = relative rate of growth at time t

A number of alternative functions would have provided an equally valid approximation to the data, but the Gompertz function had the advantages of being a generally accepted description of mammalian growth (Laird, 1966) and could be fitted using the minimum number of parameters.

Linear allometry was used to derive relative growth rates of dissected carcass tissues and chemical components of the empty body:

$$Y = aX^b \qquad \text{(Huxley, 1932; Seebeck, 1968)}$$

or in practice,

$$\log_e Y = \log_e a + b \log_e X$$

where Y = weight of dissected carcass tissue or chemical component of the empty body
X = empty body weight

Reasons behind the choice of linear allometry for this purpose were that it allowed comparison with relationships obtained by linear regression analysis on the same data, and moreover, that it had been shown elsewhere to produce the most convincing description of pig growth for pigs slaughtered over a range of ages, carcass weights,

genotypes and sexes (Evans and Kempster, 1979). Examination of MLC Commercial Product Evaluation dissection data by four different analyses led Evans and Kempster (1979) to conclude that linear allometry gave the best account of tissue growth and carcass development for 1006 pigs between pork (61 kg) and heavy pig (118 kg) slaughter weights. The authors detected a small degree of curvilinearity for total dissected carcass lean; the latter may have arisen due to the pooling of data from pigs of different sexes (gilts and castrates) and of different feed intake regimes (*ad-libitum* and restricted) for the purposes of the analysis. Dissected component weight and carcass composition in the empty body weight of initial slaughter group pigs (litters 1 and 2) were obtained by linear regression. As intercepts were not significant they were excluded so that dissected lean and chemical components were expressed as proportions of the empty body weight (Table 1.3).

TABLE 1.3: Composition of the initial slaughter group at 55 days of age (n = 6)

Empty body weight (EBW, kg)	=	0.919 live weight (kg)
Dissected lean (kg)	=	0.379 EBW (kg)
Protein (kg)	=	0.166 EBW (kg)
Lipid (kg)	=	0.106 EBW (kg)
Ash (kg)	=	0.035 EBW (kg)
Water (kg)	=	0.627 EBW (kg)
GE (MJ)	=	8.291 EBW (kg)

The equations in Table 1.3 were then used to estimate body composition at 55 days of the other 36 pigs. Daily gains of body components were calculated as the difference between start composition

and composition at slaughter, divided by days on test. These results were described as functions of pig age and live weight by means of linear regression analysis ($Y = a + bX$).

RESULTS

Of the 45 pigs (15 trios) used in this experiment, complete data sets were obtained for 42 pigs (14 boars, 14 gilts and 14 castrates). The three missing animals were discarded on health grounds:

1 boar, litter 9	-	scheduled for slaughter at 160 days of age, slaughtered at 60 days, dislocated pelvis
1 gilt, litter 13	-	scheduled for slaughter at 280 days of age, slaughtered at 270 days, spinal abscess
1 castrate, litter 8	-	scheduled for slaughter at 125 days, slaughtered at 115 days, recurring rectal prolapse.

In addition, the boar belonging to litter 2, and which weighed only 0.66 of contemporary boars (n = 13) when slaughtered at 55 days of age, was discovered *post-mortem* to have been suffering from chronic leg joint lesions. Nevertheless, as the carcass composition of this pig was commensurate with its live weight, if not its chronological age, and as this pig's data would improve regressions of body components on empty body weight for initial slaughter group pigs (used to estimate start composition of pigs slaughtered between 91 and 332 days of age) it was included with the other results.

Weights and chemical compositions of the whole empty body and dissected fractions are detailed for individual pigs in the following Appendices:

Appendix 1.1 Live weight and empty body weight at slaughter and chemical composition of the empty body

Appendix 1.2 Carcass dissected lean and dissected lean plus intermuscular fat

Appendix 1.3 Carcass subcutaneous fat and skin (plus P2 backfat depth measurement)

Appendix 1.4 Carcass bone and blood

Appendix 1.5 Head, feet and tail and non-carcass fractions.

It was not possible to include data for each sex of pig in each of the diagrams which follow. Where crowding of results on a figure would have impaired its interpetations, entire male pigs have been used as the example. (See end of Results text for Figures 1.3 onwards.)

Daily feed intake

Daily feed intakes of boars are plotted against days of age in Figure 1.3 and live weight in Figure 1.4. There was a linear increase in daily feed intake (DFI, kg fresh weight) until 140 days of age and 85 kg live weight:

21-140 days of age	DFI = 0.033 days of age (±0.0007) − 0.486 (±0.0570)	r = 0.95
4.7-85 kg liveweight	DFI = 0.046 live weight (kg) (±0.0012) + 0.347 (±0.0446)	r = 0.94

Daily feed intakes by gilts and castrates showed a similar increase relative to age and live weight:

Gilts	DFI = 0.029 days of age (±0.0008) − 0.263 (±0.0593)	r = 0.93
	DFI = 0.043 live weight (kg) (±0.0012) + 0.411 (±0.0440)	r = 0.93

Castrates	DFI = 0.035 days of age (±0.0009)	- 0.396 (±0.0656)	r = 0.94
	DFI = 0.048 live weight (kg) (±0.0013)	+ 0.416 (±0.0527)	r = 0.93

Castrates tended to have greater appetites than boars: regressions of daily feed intake on live weight suggest it was particularly at lower live weights that castrates consumed more food than boars.

Following the attainment of peak feed intakes at around 150 days of age, daily feed intakes oscillated widely about a mean intake from 160 days onwards: mean daily feed intakes were 3.97 (s.d. 0.775), 3.63 (s.d. 0.794) and 3.74 (s.d. 0.702) kg for boars, gilts and castrates respectively. The greater variation in feed intakes by gilts resulted from appetite depression during oestrus. Peak volume intakes, reached at around 150 days of age, were 0.24 litres day^{-1} per kg $W^{0.75}$ for boars and gilts, and 0.26 litres day^{-1} per kg $W^{0.75}$ for castrates.

Daily feed intakes over the entire age and live weight range were also plotted against metabolic live weight ($W^{0.75}$), but this analysis did not alter the overall pattern of daily feed intake, nor did it indicate that the latter could be described more satisfactorily as a curvilinear function of live weight.

Liveweight gain and its dissected and chemical composition

Change in live weight over time by entire male pigs is shown in Figure 1.5. A companion diagram (Appendix 1.7) details liveweight change for an individual boar (litter 13, slaughtered at 332 days of age), together with the Gompertz function fitted to this pig's data.

Parameters estimated by the application of the Gompertz function to growth curves of final slaughter group pigs (litters 14 and 15) are presented in Table 1.4.

TABLE 1.4: Estimated live weight at maturity (A), relative instantaneous growth rate (B) and point of inflection (t*) for trios of pigs slaughtered at 330 and 332 days of age

Litter	Sex	Age at slaughter (days)	Liveweight at slaughter (kg)	A (kg)	B (day^{-1})	t* (days)
14	Boar	330	199.60	225	0.0100	164
15	"	332	205.20	250	0.0091	182
14	Gilt	330	182.30	200	0.0114	141
15	"	332	205.80	225	0.0107	153
14	Castrate	330	213.70	225	0.0110	149
15	"	332	198.90	225	0.0098	167

The trio of pigs from litter 15 were slightly later maturing than the trio from litter 14 to judge by their lower 'B' values, higher 'A' values and more advanced age at t*.

Growth of dissected carcass muscle, dissected carcass fat (subcutaneous plus intermuscular) and dissected carcass bone was allometric to growth of the empty body; growth coefficients for dissected fractions are shown for boars in Figure 1.6. The growth coefficients for chemical components as allometric functions of boars' empty body weights appear in Figure 1.7. A summary of linear regression equations relating $\log_e$ component to $\log_e$ empty body weight is given in Table 1.5.

As anticipated, bone, followed by muscle, proved to be the earliest-maturing dissected fractions. Dissected fat, though later maturing, exhibited the greatest relative growth rate. There were no sex differences between growth coefficients for the dissected carcass fractions. The margin in relative growth rates between dissected muscle from boar and castrate carcasses only narrowly missed significance. However, the discrepancy in relative growth of empty body protein between boars and castrates did prove significant ($P < 0.05$).

TABLE 1.5: Linear allometric relationships between dissected carcass components and empty body weight and between chemical components of the empty body and empty body weight

$\log_e$ component (Y) = $\log_e$ a + b $\log_e$ Empty body weight (X)

	Boars (n=14):			Gilts (n=14):			Castrates (n=14):		
	b(±SE)	a(±SE)	r	b(±SE)	a(±SE)	r	b(±SE)	a(±SE)	r
Component (Y)									
(i) dissected, carcass									
muscle	0.966 *(±0.0354)*	-0.888 *(±0.1556)*	0.99	0.930 *(±0.0298)*	-0.772 *(±0.1286)*	0.99	0.860 *(±0.0391)*	-0.498 *(±0.1728)*	0.99
fat	1.401 *(±0.0764)*	-3.389 *(±0.3357)*	0.98	1.533 *(±0.0625)*	-3.797 *(±0.2700)*	0.99	1.582 *(±0.0882)*	-3.999 *(±0.3896)*	0.98
bone	0.830 *(±0.0393)*	-1.825 *(±0.1728)*	0.99	0.836 *(±0.0384)*	-1.914 *(±0.1657)*	0.99	0.809 *(±0.0386)*	-1.768 *(±0.1703)*	0.99
(ii) chemical, whole empty body									
protein	0.963† *(±0.0247)*	-1.646 *(±0.1083)*	1.00	0.927 *(±0.0208)*	-1.563 *(±0.0899)*	1.00	0.850† *(±0.0489)*	-1.271 *(±0.2159)*	0.98
water	0.862 *(±0.0311)*	-0.075 *(±0.1365)*	0.99	0.830 *(±0.0232)*	+0.008 *(±0.0999)*	0.99	0.778 *(±0.0314)*	+0.216 *(±0.1387)*	0.99
lipid	1.519 *(±0.0777)*	-3.910 *(±0.3413)*	0.98	1.626 *(±0.0478)*	-4.165 *(±0.2063)*	0.99	1.665 *(±0.0485)*	-4.318 *(±0.2142)*	0.99
ash	0.923 *(±0.0280)*	-3.024 *(±0.1228)*	0.99	0.923 *(±0.0292)*	-3.080 *(±0.1261)*	0.99	0.896 *(±0.0464)*	-2.944 *(±0.2051)*	0.98

† significantly different ($P < 0.05$)

A combination of parameters estimated by application of the Gompertz function to liveweight change in final slaughter group pigs (Table 1.4) and parameters derived by linear allometry of dissected and chemical components on empty body weight (all pigs, Table 1.5) was used to predict the pattern of daily protein and lean deposition rate with increasing empty body weight. Figure 1.8 shows predicted values for boars, Figure 1.9 gives predicted values for gilts, and those for castrates appear in Figure 1.10. The curves produced suggest that maximum protein and lean deposition rate occurs between 50 and 110 kg empty body weight for boars and 40 and 100 kg empty body weight for gilts and castrates. Predicted deposition rates rose steeply at lower empty body weights (10 to 30 kg) but were subject to a more gradual decline after 100 or 110 kg empty body weight in the approach to zero daily gain of protein and lean at mature empty body weight. Although curves for protein and lean deposition convey the impression of a change in the ratio of daily protein gain : daily lean gain, this ratio was constant within sexes: 2.17 for boars, 2.25 for gilts and 2.31 for castrates.

Further estimations were generated regarding the proportions of protein and lean in the empty body,

	Protein	Lean
boars	0.158	0.342
gilts	0.142	0.318
castrates	0.125	0.286

implying a distinct 'gradient' in protein and lean content for the different sexes of pig.

Calculated daily gains by individual pigs in live weight, empty body weight, dissected carcass lean, protein, water, lipid and ash appear in Table 1.6.

TABLE 1.6: Daily gains in live weight (LW), empty body weight (EBW), dissected lean (DL), protein (P), water (W), lipid (L) and ash (A) by boars, gilts and castrates between 55 days of age and slaughter

		Boars:							Gilts:							Castrates:						
Litter	Days[1]	LW	EBW	DL	P	W	L	A	LW	EBW	DL	P	W	L	A	LW	EBW	DL	P	W	L	A
3	36	0.643	0.638	0.213	0.126	0.384	0.092	0.026	0.695	0.673	0.251	0.103	0.371	0.103	0.023	0.735	0.700	0.255	0.128	0.402	0.118	0.027
4	36	0.704	0.660	0.249	0.123	0.434	0.038	0.031	0.544	0.506	0.162	0.094	0.289	0.058	0.020	0.782	0.719	0.260	0.126	0.340	0.128	0.028
5	68	0.776	0.754	0.198	0.117	0.291	0.208	0.026	0.713	0.697	0.197	0.113	0.303	0.166	0.024	0.760	0.731	0.161	0.088	0.230	0.210	0.022
6	68	0.912	0.869	0.318	0.155	0.383	0.225	0.033	0.666	0.636	0.162	0.092	0.253	0.198	0.020	0.794	0.766	0.237	0.120	0.316	0.192	0.026
7	69	0.724	0.697	0.236	0.111	0.295	0.136	0.024	0.743	0.717	0.191	0.107	0.271	0.255	0.025	0.722	0.697	0.174	0.110	0.259	0.201	0.030
8	71	0.726	0.702	0.205	0.105	0.293	0.255	0.027	0.694	0.673	0.229	0.105	0.256	0.186	0.026	-	-	-	-	-	-	-
9	108	-	-	-	-	-	-	-	0.828	0.809	0.248	0.120	0.342	0.306	0.029	0.848	0.822	0.233	0.114	0.328	0.346	0.031
10	110	0.704	0.681	0.295	0.122	0.376	0.150	0.023	0.780	0.742	0.270	0.115	0.356	0.208	0.023	0.764	0.724	0.248	0.112	0.343	0.239	0.025
11	140	0.898	0.860	0.324	0.162	0.435	0.197	0.032	0.820	0.800	0.275	0.123	0.333	0.295	0.027	0.925	0.895	0.305	0.135	0.381	0.339	0.033
12	176	0.829	0.794	0.237	0.126	0.353	0.254	0.027	0.819	0.792	0.205	0.097	0.284	0.354	0.021	0.683	0.663	0.152	0.077	0.228	0.315	0.017
13	230	0.793	0.771	0.226	0.108	0.312	0.236	0.022	-	-	-	-	-	-	-	0.567	0.556	0.168	0.073	0.215	0.217	0.017
14	275	0.664	0.641	0.219	0.098	0.266	0.216	0.018	0.592	0.580	0.177	0.079	0.231	0.220	0.016	0.702	0.686	0.190	0.091	0.270	0.270	0.022
15	277	0.681	0.652	0.207	0.098	0.280	0.215	0.020	0.655	0.621	0.162	0.088	0.209	0.306	0.014	0.639	0.621	0.162	0.073	0.209	0.306	0.014
Mean		0.754	0.727	0.244	0.121	0.342	0.185	0.026	0.712	0.687	0.211	0.103	0.291	0.221	0.022	0.743	0.715	0.212	0.104	0.293	0.240	0.024

[1] between 55 days of age and slaughter

Considerable variation between-sexes and between-litters was apparent from these results, but the most striking finding was the similarity in average daily protein and lean deposition rates: gilts retained 0.103 kg of protein and 0.211 kg of lean, while castrates retained 0.104 kg of protein and 0.212 kg of lean day^{-1}. As average daily water and ash gains were also very similar, the greater daily empty body gains by castrates were attributable to their 0.086 higher lipid deposition rate. Entire male pigs showed the most rapid deposition rates for protein, lean and water at averages of 0.121, 0.244 and 0.342 kg day^{-1}. Lipid deposition rate was 0.19 lower in boars than gilts and 0.30 lower in boars than in castrates.

Figure L11 shows the alteration in lipid : protein ratio of the daily empty body gain with increasing live weight. In the case of entire males, this ratio never exceeded 2.2 : 1 throughout the whole slaughter range (20 to 200 kg live weight). The exceptionally fast-growing, lean boar from litter 11 gained only 1.22 units of lipid for each unit of protein deposited between 55 and 195 days of age. Lipid : protein ratio in the empty body gain showed marked divergence for the different sexes of pig after about 125 days of age or 70 kg live weight. Within slaughter groups, a low lipid : protein ratio indicated one of two eventualities: (i) an animal depositing protein rapidly and discriminating against lipid, or (ii) an animal depositing both protein and lipid at below average rates. High lipid : protein ratio relative to age was usually associated with particularly disappointing protein deposition rate, but less commonly, resulted from a very high rate of lipid gain (principally by castrated male pigs).

Figure 1.12 depicts water : protein ratio in the daily empty body gain as a function of mean live weight. With the exception of litters

5 to 8 (slaughtered around 125 days of age), water : protein ratio decreased rapidly until 195 days of age or approximately 150 kg live weight, and on reaching this stage, the ratio then levelled off at an average value of 2.85 units of water per unit of protein.

Ash : protein ratio was constant with both age and live weight at 0.22 : 1.

Protein mass and daily protein deposition rate

Change in protein mass over time is shown in Figure 1.13, while protein mass with respect to empty body weight appears in Figure 1.14. Whereas empty body protein against empty body weight was satisfactorily described by linear regression (see equation below), empty body protein against age deviated from linearity at more advanced ages, and the fitted linear regression line has not been included on Figure 1.13. From around 165 days of age and 100 kg live weight, entire male pigs contained more total body protein than gilts or castrates relative to both age and empty body weight.

There were no significant differences between boars and gilts in total protein as a proportion of empty body weight,

Boars and gilts (n=28)	Total body protein (kg)	= 0.144 EBW (kg) (±0.0047)	+ 1.051 (±0.5237)	r = 0.99

but castrated male pigs contained less total protein per unit empty body weight ($P < 0.05$)

Castrates (n=14)	Total body	= 0.124 EBW (kg) (±0.0061)	+ 1.804 (±0.6955)	r = 0.98

Using the allometric equations detailed previously the total body protein mass at maturity was predicted for the six pigs in the final slaughter group:

Boars	34.22	(litter	14)	and	37.78	(litter	15)
Gilts	27.41	"	"	and	30.57	"	"
Castrates	27.05	"	"	and	32.98	"	"

The heavier, later-maturing trio in litter 15 were destined to have higher protein masses at maturity.

Figures 1.15 and 1.16 show the pattern of daily protein deposition rate against mean day and mean live weight respectively. No distinct pattern emerged other than the supremacy of entire males at higher ages and live weights and the decline in deposition rate for each sex, from approximately 195 days of age (mean age, 125 days) and 150 kg live weight (mean live weight, 90 kg), as maturity was approached. The onset and rate of decline in daily protein gain was earlier and more abrupt for a) gilts and castrates than for boars, and b) for animals of lower protein growth potential and mature protein mass. Correlation coefficients for daily protein deposition rate against age and live weight were poor, though marginally improved by fitting a linear regression rather than by fitting a "shallow" quadratic. The advantage of a straight-line function over a quadratic function was that it provided a more appropriate explanation of daily protein deposition rate in the younger animals. Three small female pigs (reared under identical conditions to animals in this experiment as part of the trial reported in Section 2C; indicated in Figures by the symbol (▲)) deposited protein at the rate of 80 g day^{-1} between 25 and 70 days of age and at a mean live weight of 16.4 kg (roughly 0.075 of maturity). The least-mature animals in the present experiment for which protein growth rates were calculated (litters 3 and 4) deposited an average of 117 g protein day^{-1} between 55 and 91 days of age and at a mean live weight of 31.3 kg (0.14 of maturity). Thus, while it is evident

that daily protein deposition rate increases with time and live weight in young animals post-weaning, these results suggested that a plateau in deposition rate could be reached by 55 days of age or 20 kg live weight. Subsequent to this stage, only minor increases in daily protein gain took place.

For all pigs, the relationships between daily protein deposition rate (DPDR, kg) and age and live weight were

All pigs (n=36)	DPDR =	-0.0002 mean day (±0.00007)	+ 0.139 (±0.0092)	r = 0.48
All pigs (n=36)	DPDR =	-0.0002 mean live weight (±0.00012)	+ 0.125 (±0.0086)	r = 0.30

Regression coefficients for boars, gilts and castrates were not significant for DPDR upon age or live weight, but intercepts were always significant; the latter were of similar magnitude for boars and castrates but lower for gilts:

	Mean age	Mean live weight
Boars	0.144	0.132
Gilts	0.126	0.116
Castrates	0.148	0.125

Figure 1.17 illustrates the change in nitrogen retention per kg mean $LW^{0.75}$ day^{-1} against mean live weight. The rate of linear decrease in nitrogen retention per unit metabolic live weight (NR) was independent of sex of pig,

All pigs (n=36)	NR =	-0.011 mean live weight (±0.0009)	+ 1.582 (±0.0668)	r = 0.89

but appeared to underestimate nitrogen retentions by younger pigs.

The relationship between dissected carcass lean and total body protein

Dissected carcass lean (DL, kg) increased linearly with increase in total body protein ($r = 0.99$). Intercepts were not significant and regressions have therefore been forced through the origin.

Boars (n=14)	DL =	2.150 total body protein (±0.0332)
Gilts (n=14)	DL =	2.277 total body protein (±0.0320)
Castrates (n=14)	DL =	2.217 total body protein (±0.0283)

There were no significant differences between regression coefficients for the three sexes of pig. The relationship between dissected carcass lean and total body protein for all pigs is given below.

All pigs (n=42)	DL =	2.206 total body protein (±0.0195)

Lean mass and daily lean deposition rate

Change in lean mass over time is shown in Figure 1.18, and the change in lean mass with empty body weight is described in Figure 1.19. Entire male pigs contained higher lean mass for age than gilts or castrates, but all pigs contained the same proportion of dissected lean (DL, kg) in the empty body

All pigs (n=42)	DL =	0.305 EBW (±0.0100)	+ 2.556 (±1.1173)	r = 0.98

Dissected carcass lean at maturity was predicted (using the derived allometric relationship between carcass muscle and empty body weight) for the six pigs in the final slaughter group:

Boars	73.23	(litter	14)	and	81.88	(litter 15)
Gilts	61.45	"	"	and	68.57	" "
Castrates	61.86	"	"	and	61.86	" "

Greater live weight at maturity was associated with a larger predicted lean mass at maturity.

Figures 1.20 and 1.21 show the pattern of daily lean deposition rate against mean age and mean live weight. The overall shape of daily lean gain was very similar to that of daily protein gain, and incurred the same problem in its description. Variation between litters within sexes was such that linear regression of daily lean deposition rate (DLDR, kg) on mean age and mean live weight represented the most useful approximation to the data.

All pigs (n=36)	DLDR =	-0.0003 mean day (±0.00018)	+ 0.258 (±0.0231)	r = 0.22
All pigs (n=36)	DLDR =	-0.0002 mean live weight (±0.00028)	+ 0.236 (±0.0203)	r = 0.12

Intercepts for the three sexes of pig were as follows,

	Mean age	Mean live weight
Boars	0.265	0.248
Gilts	0.237	0.219
Castrates	0.277	0.251

Factors affecting daily protein and lean gains

Body protein and carcass lean gains were inextricably linked such that animals with higher daily protein gains were those with higher daily lean gains:

All pigs (n = 36) DPDR = 0.386 DLDR + 0.023 (±0.0379) (±0.0086) r = 0.86

and there was a highly significant correlation between dissected carcass lean and total body protein. Certain litters were exceptional in their protein and lean gains: the boar, gilt and castrate from litter 11 deposited 0.162, 0.123 and 0.135 g protein day^{-1} (between 55 and 195 days of age) and 0.324, 0.275 and 305 g lean day^{-1}; each deposition rate represented the maximum rate measured for the particular sex of pig. Among their contemporaries, the boar and castrate from litter 6 achieved high protein and lean growth rates between 55 and 123 days of age (0.155 and 0.120 g protein day^{-1}; 0.318 and 0.237 g lean day^{-1}) although their female sib was very disappointing in her protein and lean growth performance (0.092 g protein and 0.162 g lean day^{-1}).

Conversely, pigs from litters 5, 7 and 8, slaughtered at the same age as litter 6, exhibited low protein and lean growth potential; their poor daily protein and lean deposition rate cannot be accounted for by abnormally low weight for age or circumscribed voluntary feed intakes. Rather, these pigs seemed to partition energy intake toward lipid gain or heat loss. As these were the first batch of pigs to enter the experiment, they may have been of a slightly different background to later batches.

Daily protein and lean gains were related to daily empty body-weight gains (DEBWG). There was a tendency for high protein and lean deposition rates to accompany high daily empty bodyweight gains, this trend being more pronounced for gilts and castrates than for boars.

All pigs (n = 36)	DPDR = 0.173 DEBWG - 0.014	(±0.0289) (±0.0206)	r = 0.71
All pigs (n = 36)	DLDR = 0.373 DEBWG - 0.042	(±0.0676) (±0.0483)	r = 0.68

Daily dry matter intake (DDMI, kg) did not influence either protein or lean gains. As crude protein mirrored daily feed intake (crude protein content of the diet remaining constant throughout), this parameter did not affect protein or lean increment.

All pigs (n = 36)	DPDR = -0.008 DDMI + 0.128	(±0.0059) (±0.0152)	r = 0.14
All pigs (n = 36)	DLDR = -0.004 DDMI + 0.231	(±0.0135) (±0.0350)	r = 0.04

These equations suggest that over the whole range of pig ages and live weights, daily protein and lean gains were not limited by feed (or protein) intake. Nevertheless, this method of assessing the adequacy of feed intake in achievement of maximum protein and lean growth rates masks the probable restraint on protein deposition rate in juvenile pigs exerted by appetite. In contrast, daily lipid gains (DLG, kg) were a highly positive function of dry matter intake; differences between sexes in this response were not significant.

All pigs (n = 36)	DLG = 0.109 DDMI - 0.061	(±0.0126) (±0.0326)	r = 0.82

Distribution of protein in the whole empty body

Figure 1.22 indicates the distribution of total protein in the empty bodies of boars, gilts and castrates slaughtered between 52 and 332 days of age.

To express a component as a proportion of a whole which contains that component is unsatisfactory from a statistical viewpoint,

however, the alternative procedure of using a whole which is exclusive of the component was considered even less suitable, and the former method was employed.

The dissected lean plus intermuscular fat from boar carcasses contained 0.527 of total body protein, a significantly lower proportion ($P < 0.05$) than found for gilt and castrate dissected lean plus intermuscular fat (0.564 and 0.576 respectively). Conversely, the skin dissected from boar carcasses contained a higher proportion of total body protein (0.139) than skin from gilt carcasses (0.107, $P < 0.05$) and castrate carcasses (0.091, $P < 0.001$). Distribution of total body protein in carcass subcutaneous fat, carcass bone, HFT, NC and blood did not differ significantly between pigs of different sexes. Similarly, carcass protein as a proportion of total protein was constant at 0.804 (non-carcass protein, 0.196 of total body protein) irrespective of sex or age of pig.

The standard errors associated with proportions of total protein in body fractions will have been influenced to a certain extent by the large range in pig ages and by differences between litters within sexes.

Distribution of half-carcass dissected lean between carcass joints

Weights of dissected lean in the hand, collar, rib back, rib streak, rump back, rump streak and ham joints are given in Appendix 1.6. The proportion of total dissected lean (in the left carcass side) pertaining to each joint is shown in Figure 1.23. Only two of the sex differences in distribution of dissected lean were significant: boar collar joints contained a greater proportion of side dissected lean than gilt collar joints (0.217 vs 0.193, $P < 0.05$), while rump streak joints in boar sides contained a lower proportion of dissected lean than rump streak joints in gilt sides (0.060 vs 0.073, $P < 0.05$). It is likely that

the larger standard errors associated with proportions of side dissected lean in various joints reflect differences in age within sexes, for example, the difference in dissected lean content of the collar joint between boars and gilts would become more exaggerated at greater ages and side weights.

Efficiency of dietary protein utilisation for protein deposition

Efficiency of dietary protein utilisation for protein deposition was assessed by calculation of gross nitrogen utilisation (GNU), the latter being the ratio of nitrogen retained day^{-1} to nitrogen consumed day^{-1}. GNU was then plotted against nitrogen intake (g day^{-1}) to produce the relationship shown in Figure 1.24. The decline in efficiency of nitrogen utilisation with increase in nitrogen intake proceeded at different rates for the three sexes of pig:

Boars (n=12)	GNU = -0.0030 NI (±0.00046)	+ 0.506 (±0.04336)	r = 0.89
Gilts (n=12)	GNU = -0.0028 NI (±0.00038)	+ 0.449 (±0.0337)	r = 0.91
Castrates (n=12)	GNU = -0.0032 NI (±0.00056)	+ 0.492 (0.0563)	r = 0.86

The regression slope for castrates was significantly steeper than that for boars ($P < 0.05$) and gilts ($P < 0.001$), suggesting that efficiency of utilisation of dietary protein decreased more rapidly for castrated males as nitrogen intake rose, that is, with increasing age and live weight.

Backfat depth (P2) as a predictor of carcass dissected lean and dissected fat

Backfat depth measurements were taken on cold carcasses at 6.5 cm from the dorsal mid-line at the head of the last rib.

The relationship between backfat depth (P2, mm) and live weight at slaughter was as follows,

All pigs (n=42)	P2 =	0.220 live weight (kg) (±0.0066)

the non-significant constant having been suppressed. Thus, for pigs fed to appetite, a kilogramme increase in live weight was accompanied by a 0.22 mm increase in P2.

Backfat depth at P2 produced quite acceptable predictions of percentage carcass lean and percentage carcass fat. There were no significant differences between sexes of pigs in this respect and the data have been combined.

All pigs (n=42)	% lean in carcass =	61.221 - 0.494 P2 (mm) (±1.0339) (±0.0395)	r = 0.89
All pigs (n=42)	% fat in carcass =	17.573 + 0.711 P2 (mm) (±1.3591) (±0.0519)	r = 0.91

No improvement in this relationship was to be gained by addition of live weight to the regression. The magnitude of the intercept in the equation relating % fat in carcass to P2 was unexpectedly high, but was explained by the occurrence of a considerable percentage of fat in the carcass of smaller pigs (litters 1 and 2, slaughtered at 55 days and around 20 kg live weight) in conjunction with a low P2 measurement, the corollary of which is that P2 does not reflect carcass fatness in animals below the usual range of slaughter weights.

A more satisfactory description of carcass composition was obtained by regressing weights of dissected lean and fat on P2 and live weight at slaughter.

All pigs (n=42)

Dissected carcass lean (kg) = 2.406 (±0.8125) − 0.523 P2 (mm) (±0.0866) + 0.409 LW (kg) (±0.0201) r = 0.99

All pigs (n=42)

Dissected carcass fat (kg) = −9.209 (±1.3761) + 0.775 P2 (mm) (±0.1466) + 0.191 LW (kg) (±0.0340) r = 0.98

Partitioning of energy retained between protein and lipid

Figure 1.25 shows the weight of protein deposited, and the energy content of protein deposited, between 55 days of age and slaughter as a function of total metabolisable energy intake. The companion diagram (Figure 1.26) shows energy retained as lipid as a function of total ME intake. Clearly, a greater proportion of the energy retained by boars was as protein energy, while castrates and gilts retained very much more of their energy intake as lipid.

Estimation of energy requirement for maintenance and efficiencies of conversion of metabolisable energy to body protein and body lipid

Metabolisable energy requirement for maintenance (ME_M) was estimated by two methods:

(i) extrapolation to metabolisable energy intake (MEI) at zero energy retention

$$MEI = ME_M + \frac{1}{k_w} ER$$

where ER = energy retained as protein plus lipid

k_w = efficiency of energy retention above maintenance

(ii) multiple regression of metabolisable energy intake upon energy required for maintenance together with the total costs of protein and lipid deposition, as proposed by Kielanowski (1966)

$$MEI = ME_M + \frac{1}{k_p} P + \frac{1}{k_l} L$$

where P = energy retained as protein
L = energy retained as lipid
k_p = efficiency of energy utilisation for protein deposition
k_l = efficiency of energy utilisation for lipid deposition

Application of this equation provides an estimate of energy for maintenance when neither protein nor lipid are being deposited.

Both methods have statistical shortcomings (Fowler, 1978), method (i) because it ignores the substantial lipid mobilisation, allied to protein deposition, at zero energy retention, and method (ii) because it assumes constant efficiencies of energy utilisation for tissue deposition and treats as independent variables two parameters which are usually inversely correlated (daily protein gain and daily lipid gain).

Initially, all calculations were made on the basis of metabolisable energy intake and energy retained (or protein and lipid energy retained) per kg mean live weight (between 55 days of age and slaughter) per day.

Employing method (i), considerable differences emerged between sexes in both ME_M and ER:

Boars (n=12)	MEI = 1.829 ER (±0.2726) + 0.230 (±0.0471)	r = 0.89
Gilts (n=12)	MEI = 1.961 ER (±0.5241) + 0.174 (±0.0471)	r = 0.74
Castrates (n=12)	MEI = 2.596 ER (±0.4191) + 0.087 (±0.0825)	r = 0.88

Estimates of ME_M for gilts and castrates were not significant, while the value of k_w obtained for castrates (0.385) was very low in itself, and considerably below the values obtained for boars (0.547) and gilts (0.510). Although ME_M estimates accorded with the expected order of magnitude, that is, highest for boars, lowest for castrates and intermediate for gilts, the estimates *per se* were held to be inaccurate and the data for all three sexes were pooled.

All pigs (n=36) $\quad MEI = 2.033\ ER \pm 0.2357 + 0.187 \pm 0.0444 \quad r = 0.82$

The above relationship between metabolisable energy intake (MJ per kg mean LW day^{-1}) and energy retained (MJ per kg mean LW day^{-1}) is depicted graphically in Figure 1.27. At zero energy retention, metabolisable energy intake was 0.187 MJ per kg mean live weight day^{-1} (equivalent on a metabolic live weight basis to 0.535 MJ ME per kg mean $LW^{0.75}\,day^{-1}$).

The pooled estimate of ME_M was then subtracted from daily MEI and the remaining energy partitioned between protein and lipid deposited using linear regression.

All pigs (n=36) $\quad MEI - ME_M = 3.727\ P \pm 0.3063 + 1.398\ L \pm 0.1219$

Efficiency of energy utilisation for protein deposition (k_p) can be calculated from this equation as 0.27, equivalent to a total cost of protein deposition of 87.6 MJ ME per kg protein. Efficiency of energy utilisation for lipid deposition (k_l) is 0.71 and the energy cost of lipid deposition is estimated at 54.9 MJ ME per kg lipid.

Using method (ii), multiple regression of MEI (per kg mean LW day^{-1}) upon energy gained as protein and lipid produced the following equations:

Boars (n=12)	MEI =	3.267 P (±0.3932)	+	1.333 L (±0.2258)	+ 0.215 (±0.0328)	r = 0.95
Gilts (n=12)	MEI =	4.175 P (±0.6450)	+	0.949 L (±0.4137)	+ 0.209 (±0.0663)	r = 0.90
Castrates (n=12)	MEI =	3.788 P (±0.7406)	+	1.749 L (±0.5881)	+ 0.156 (±0.0828)	r = 0.90

Once again, although the estimates of ME_M fell into the anticipated sequence, the relationships derived were not altogether satisfactory: estimated ME_m for castrates was not significant and efficiency of energy utilisation for lipid deposition (k_l) by gilts exceeded unity.

When data for the three sexes were pooled, the equation became

All pigs (n=36)	MEI =	3.704 P (±0.3489)	+	1.373 L (0.2102)	+ 0.191 (±0.0325)	r = 0.91

suggesting efficiencies of conversion of energy intake to body protein of 0.27 and to body lipid of 0.73. Estimated ME_M at zero protein and lipid deposition was 0.191 MJ per kg mean LW day^{-1} (equivalent to 0.545 MJ per kg mean $LW^{0.75} day^{-1}$). By this method, energy cost of protein deposition is estimated as 87.0 MJ ME per kg protein, while that of lipid is 54.0 MJ ME per kg lipid.

Method (ii) was repeated with transformed data, such that metabolisable energy intake and protein energy and lipid energy retained were expressed on the bases of

per kg mean metabolic live weight day^{-1}

per kg mean protein mass day^{-1}

per kg mean lean mass day^{-1}

per kg mean fat-free body mass day^{-1}

Calculation of ME_M by regression of MEI per kg mean $LW^{0.75}$ day^{-1} on protein and lipid energy per kg mean $LW^{0.75}day^{-1}$ lowered the correlation coefficient and produced a very high estimate of ME_M per kg mean $LW^{0.75}$ day^{-1}; this method was therefore rejected.

The next three parameters were used as bases for the calculation of ME_M, k_p and k_l in order to test the hypothesis that maintenance requirements are governed largely by an animal's protein, lean or fat-free mass rather than its empty body or live weight. Implicit in this hypothesis is the assumption that lipid, water and ash, once deposited, require minimal "upkeep" energy expenditure whereas the energy costs of protein turnover increase with each increment of protein to the protein mass. This method of calculating ME_M therefore relates maintenance requirements to the mass of the most metabolically-active tissue.

For each sex and for all pigs combined, multiple regression of MEI per kg mean lean mass or fat-free body mass produced unacceptably wide variation in estimated k_p and k_l in conjunction with a worsening in correlation coefficient (particularly for castrated males). Further, the use of protein mass as a parameter for gilts and castrates elevated k_l values above unity. The only circumstance in which protein mass provided a suitable basis for calculation of ME_M was that of entire male pigs,

Boars (n=12)	MEI	=	2.935 P (±0.4803)	+	1.426 L (±0.2446)	+	1.438 (±0.2424)	r = 0.93

suggesting an ME_M of 1.438 MJ per kg mean protein mass day^{-1}, an efficiency of conversion of energy to body protein of 0.34 and an efficiency of energy conversion to body lipid of 0.70. Corresponding

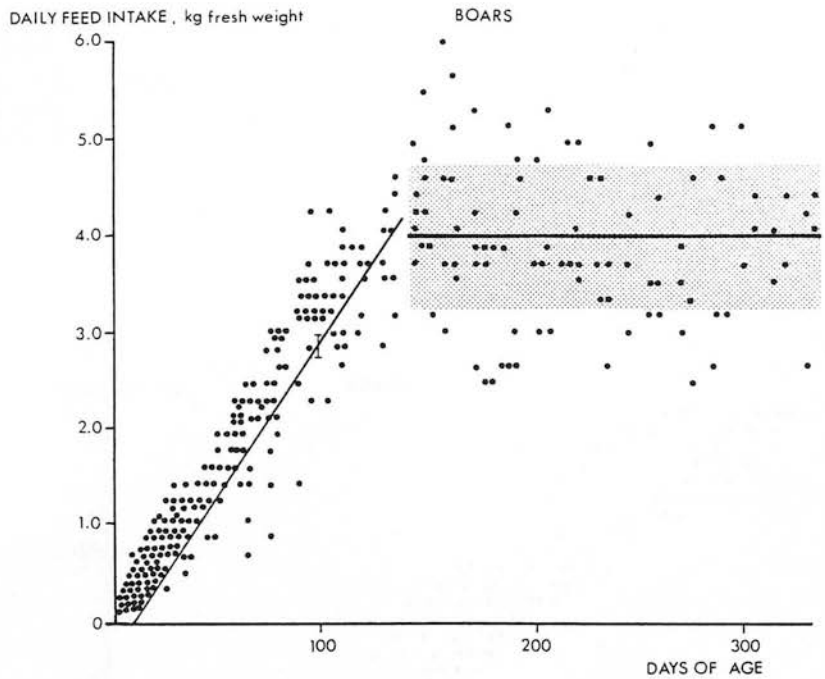


FIGURE 1.3: Daily feed intake (kg, fresh weight) by entire male pigs fed to appetite against days of age (n=14).

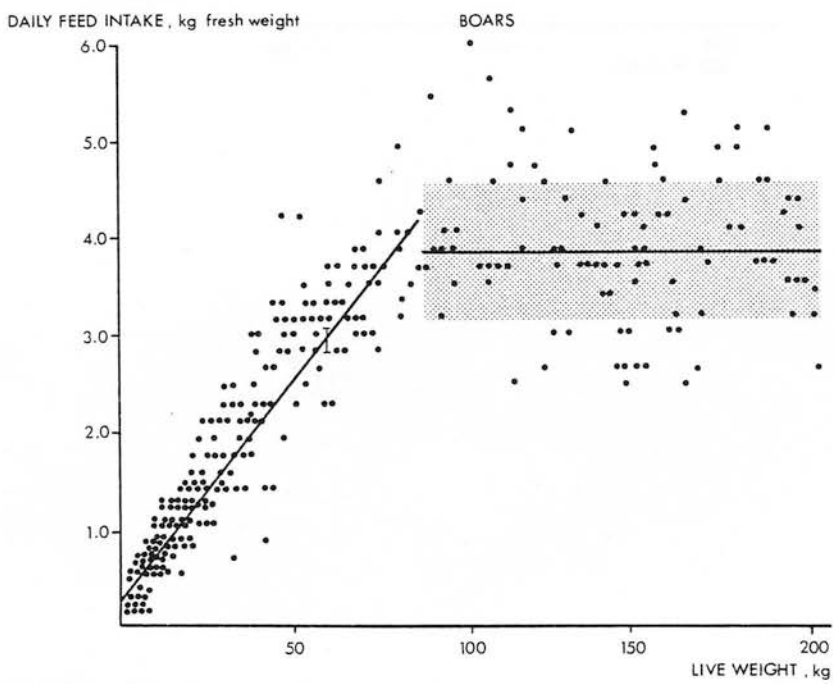


FIGURE 1.4: Daily feed intakes (kg, fresh weight) by entire male pigs fed to appetite against live weight (n=14).

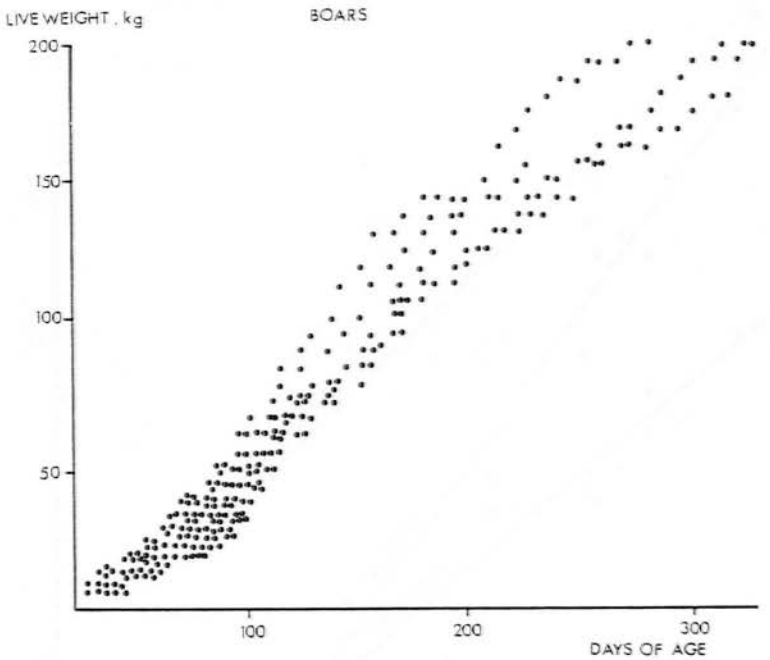


FIGURE 1.5: Change in live weight over time by entire male pigs from 21 to 332 days of age (n=14).

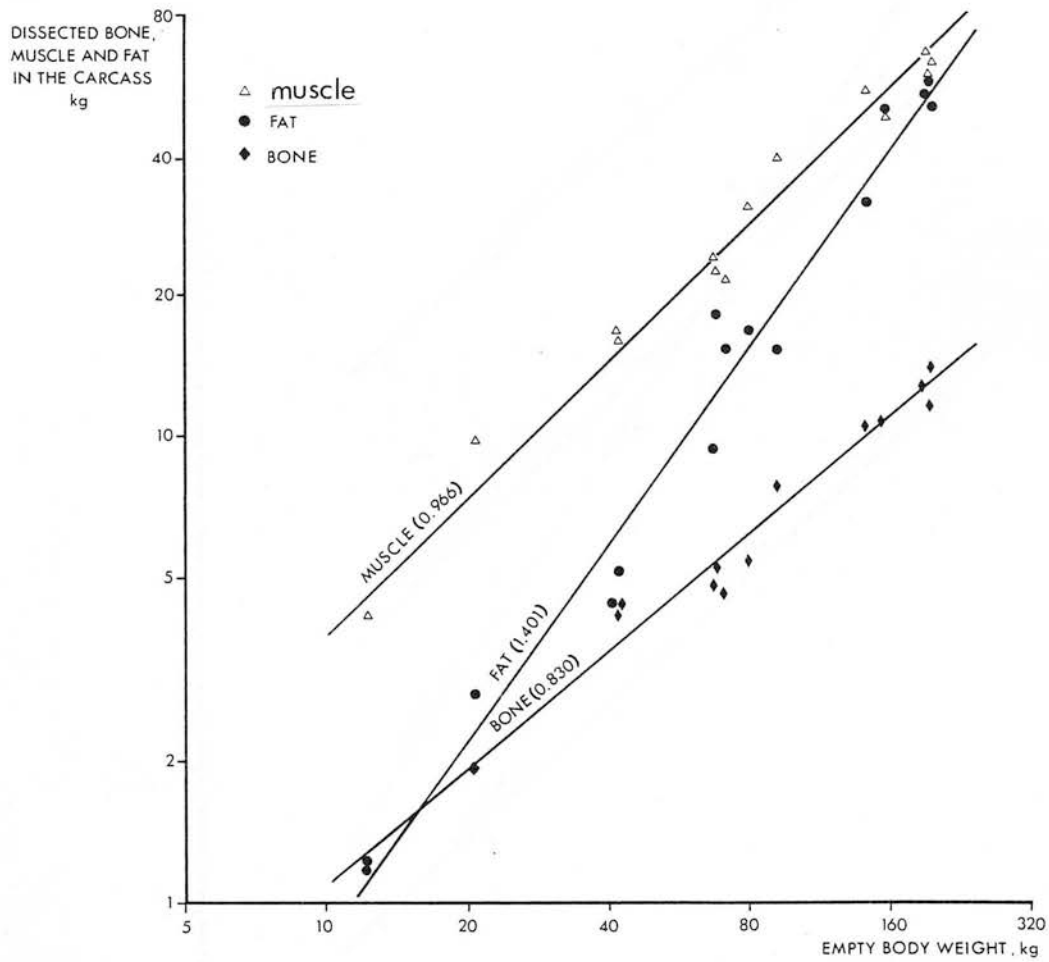


FIGURE 1.6: Growth coefficients for dissected carcass muscle, fat and bone in entire male pigs of 20 to 200 kg live weight (n=14).

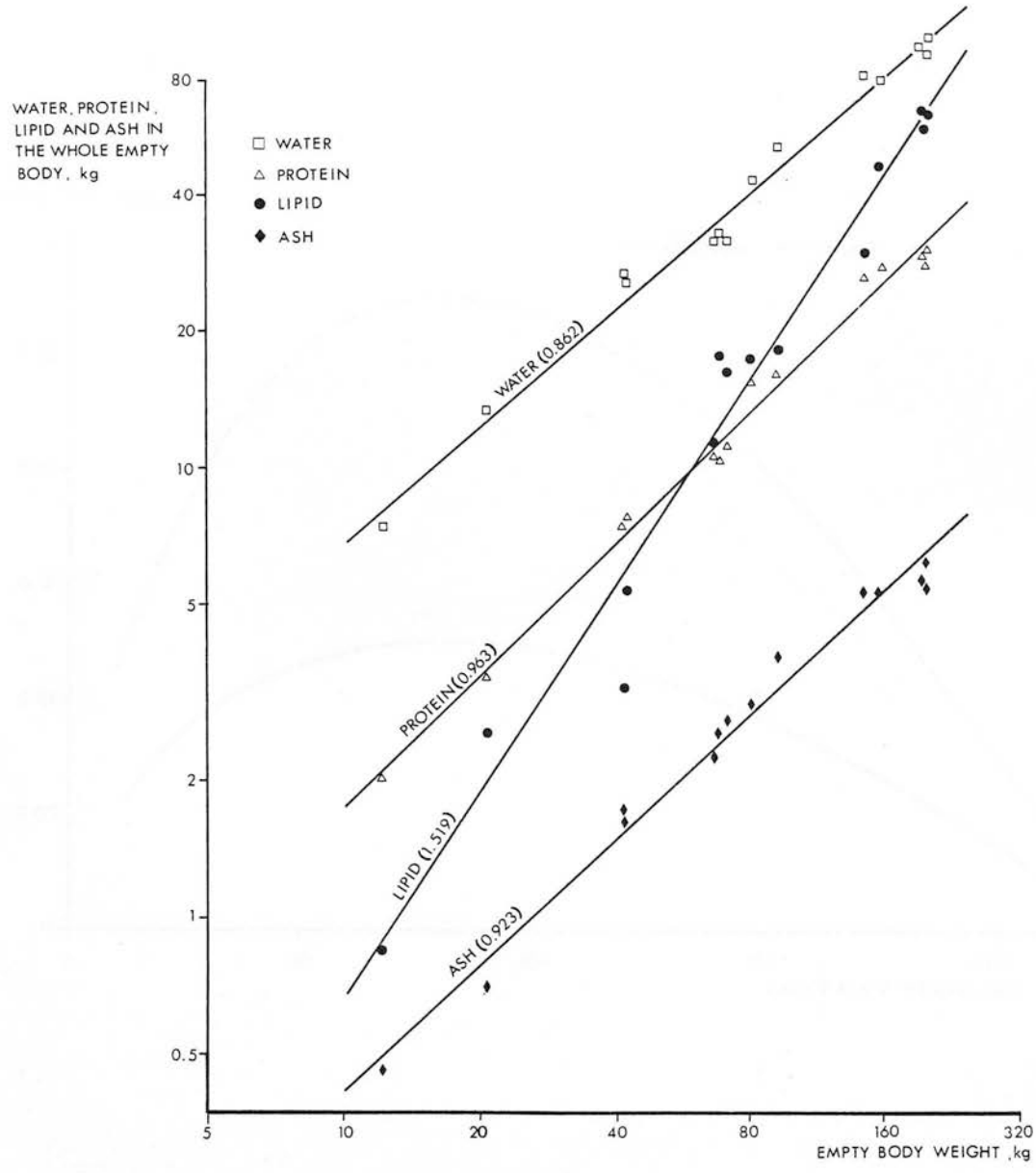


FIGURE 1.7: Growth coefficients for empty body protein, water, lipid and ash in entire male pigs of 20 to 200 kg live weight (n=14).

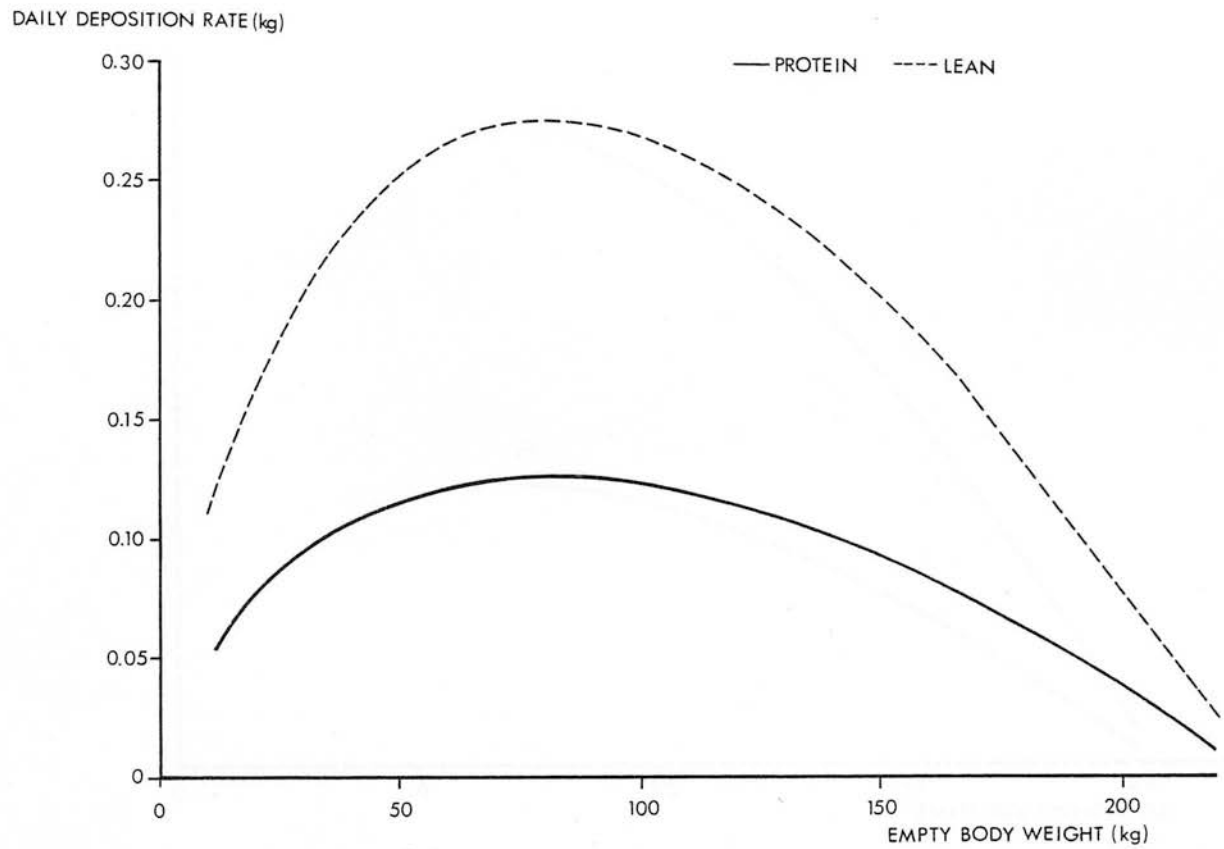


FIGURE 1.8: Predicted daily protein and lean deposition rates for boars as a function of empty body weight.

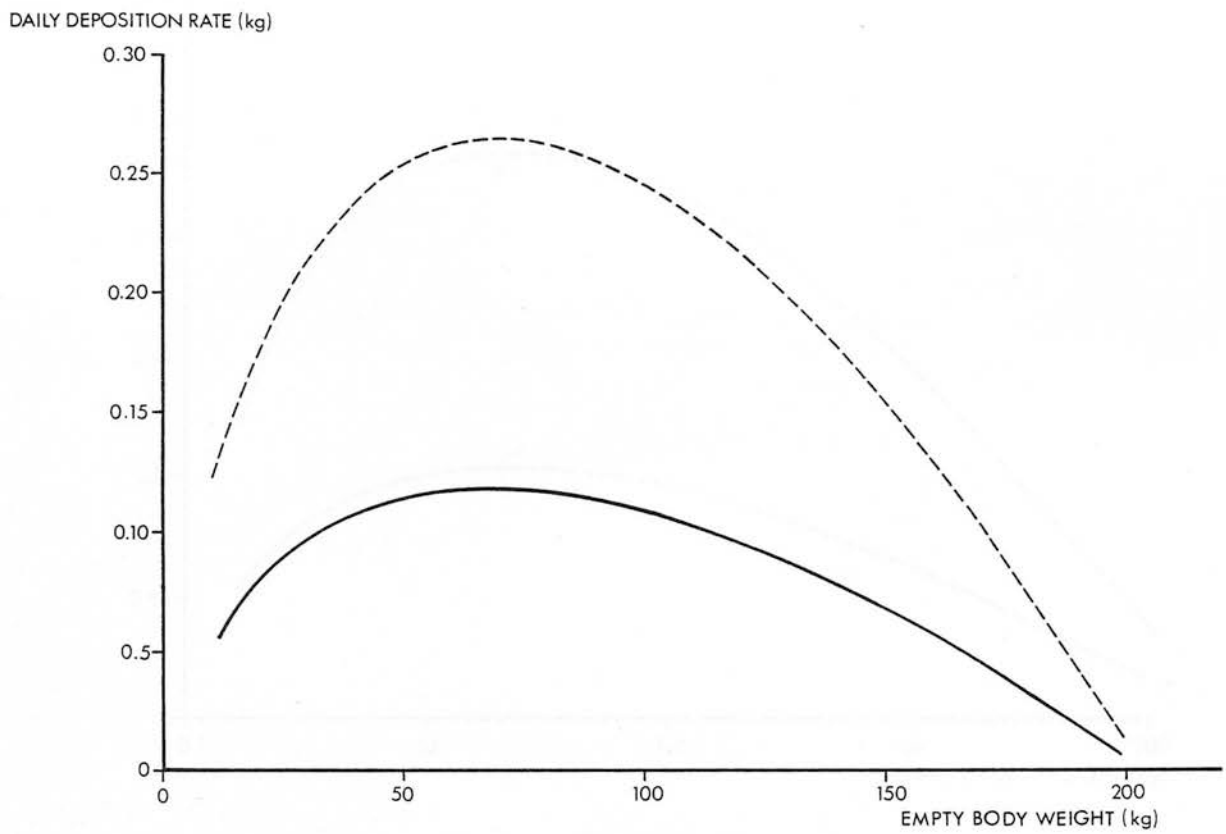


FIGURE 1.9: Predicted daily protein and lean deposition rates (kg) for gilts as a function of empty body weight.

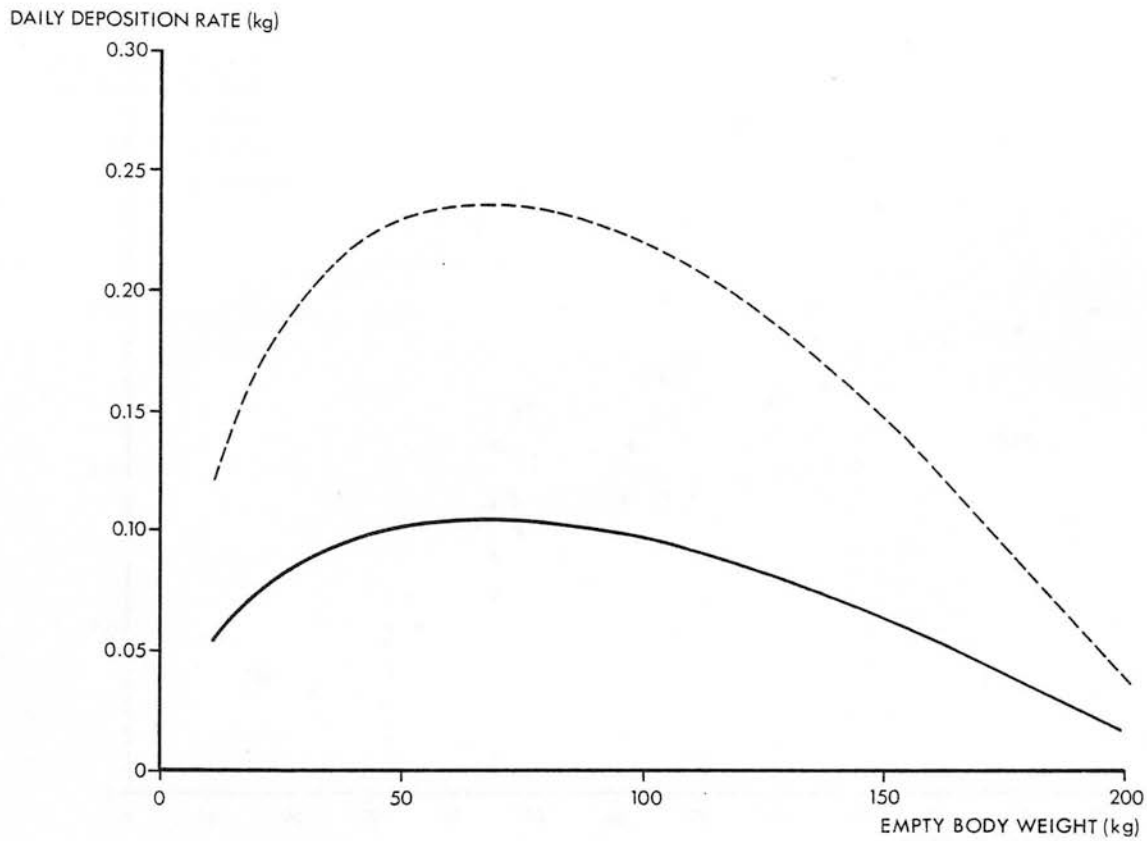


FIGURE 1.10: Predicted daily protein and lean deposition rates (kg) for castrates as a function of empty body weight.

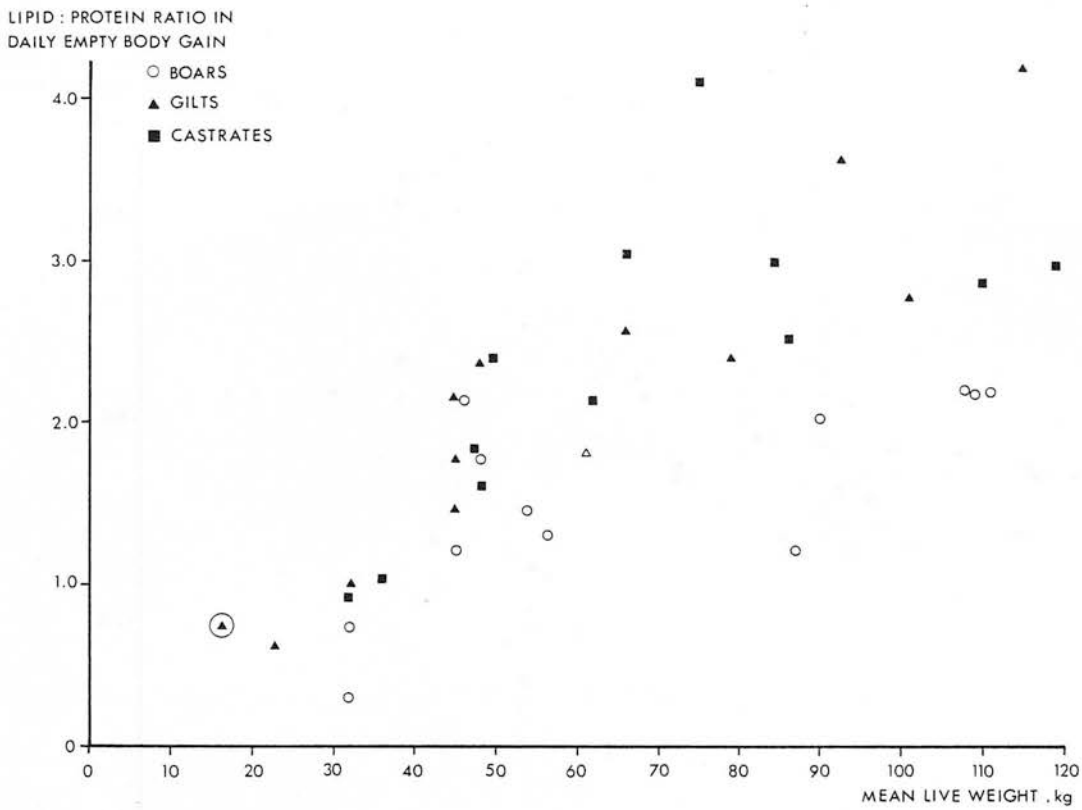


FIGURE 1.11: Lipid : protein ratio in the daily empty body weight gain of boars, gilts and castrates as a function of mean live weight between 55 days of age and slaughter.

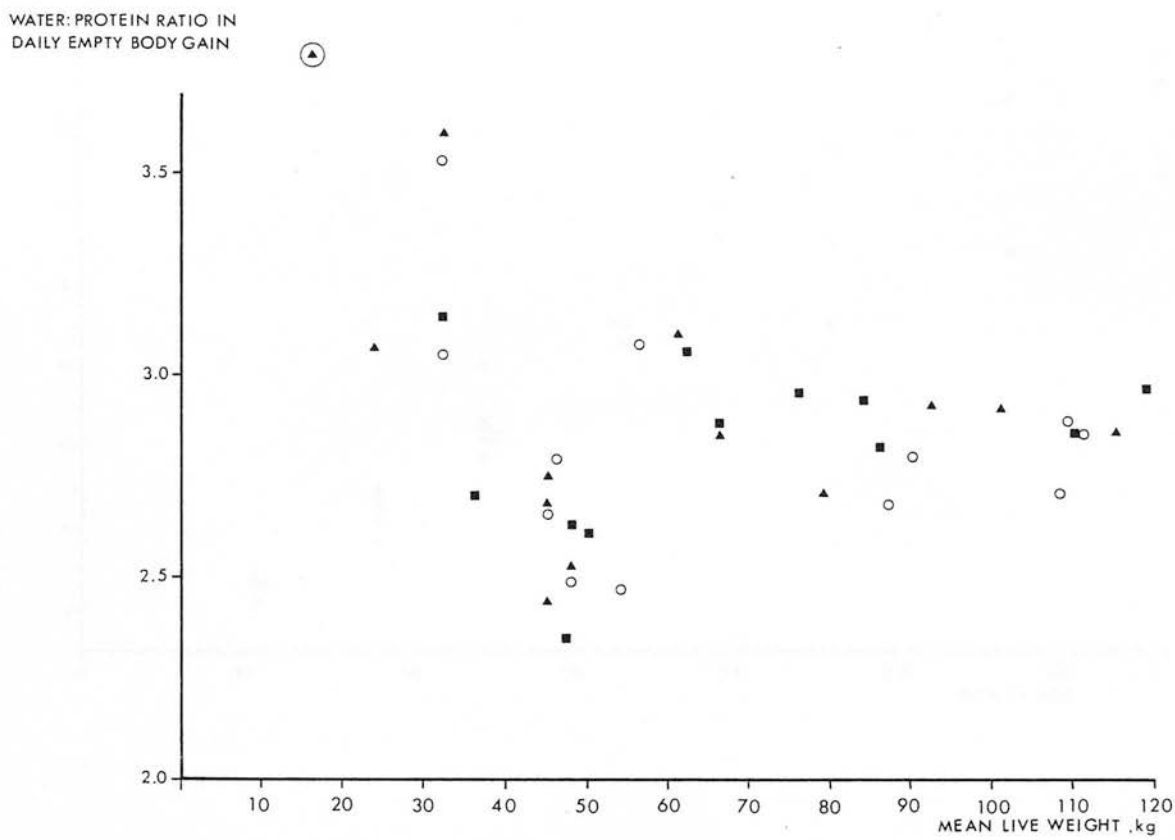


FIGURE 1.12: Water : protein ratio in the daily empty bodyweight gain of boars, gilts and castrates as a function of mean live weight between 55 days of age and slaughter.

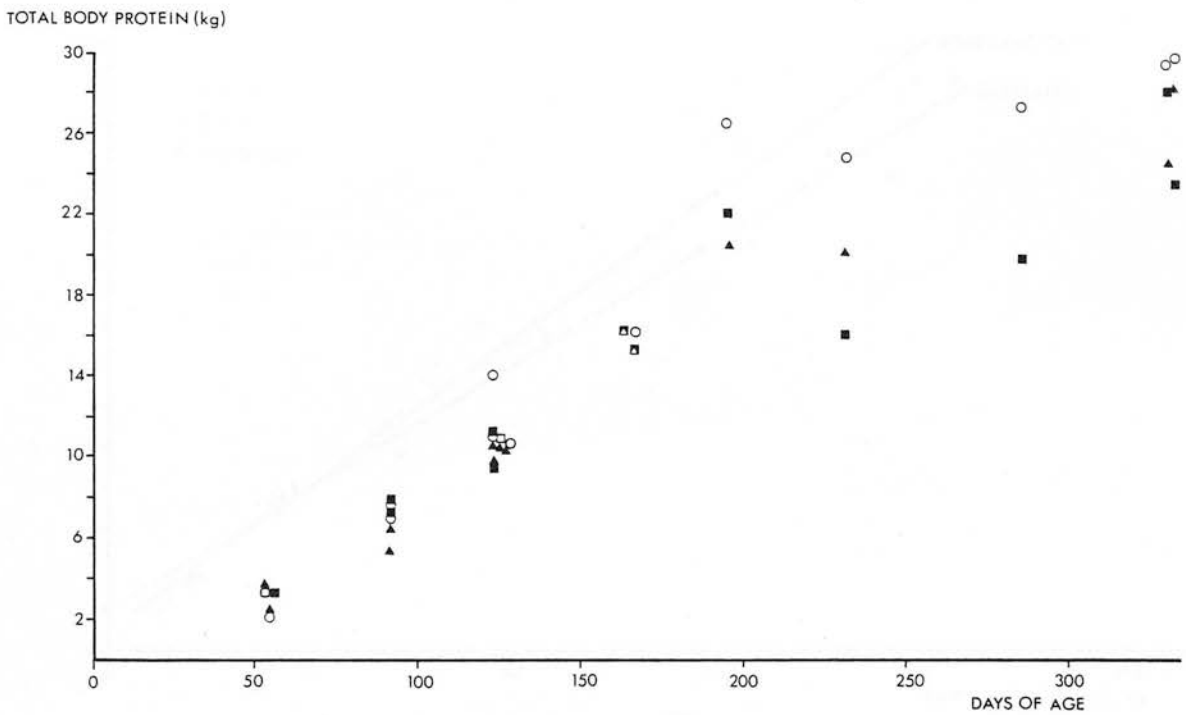


FIGURE 1.13: Total body protein (kg) as a function of age for boars, gilts and castrates (n=42).

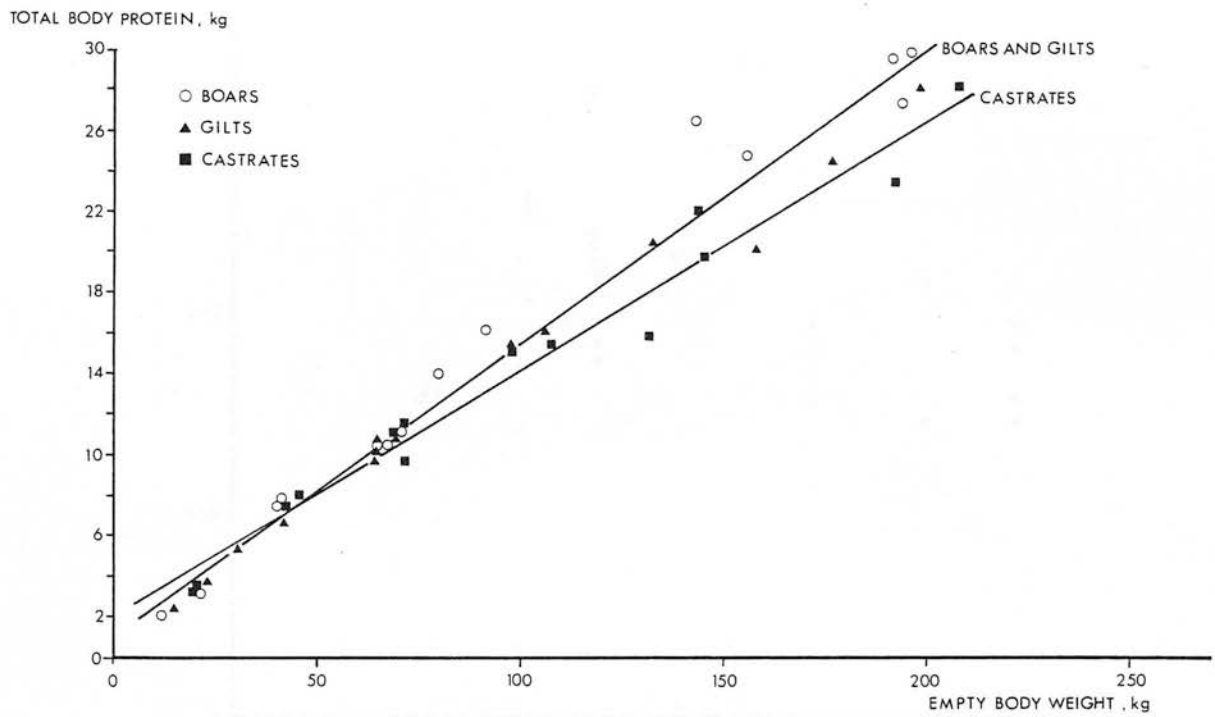


FIGURE 1.14: Total body protein (kg) as a function of empty body weight (kg) for boars, gilts and castrates (n=42).

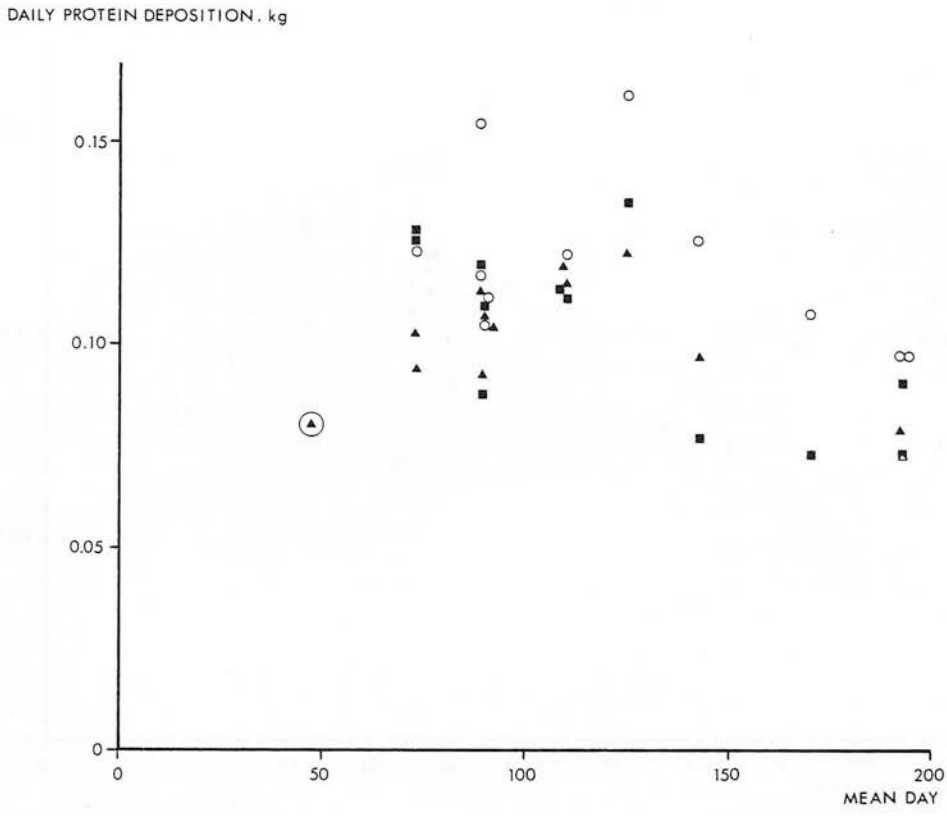


FIGURE 1.15: Daily protein deposition rate (kg) against mean day (between 55 days of age and slaughter) for boars, gilts and castrates (n=36).

[the symbol (▲) represents a mean value for female pigs (n=3) from the experiment reported in Section 2C]

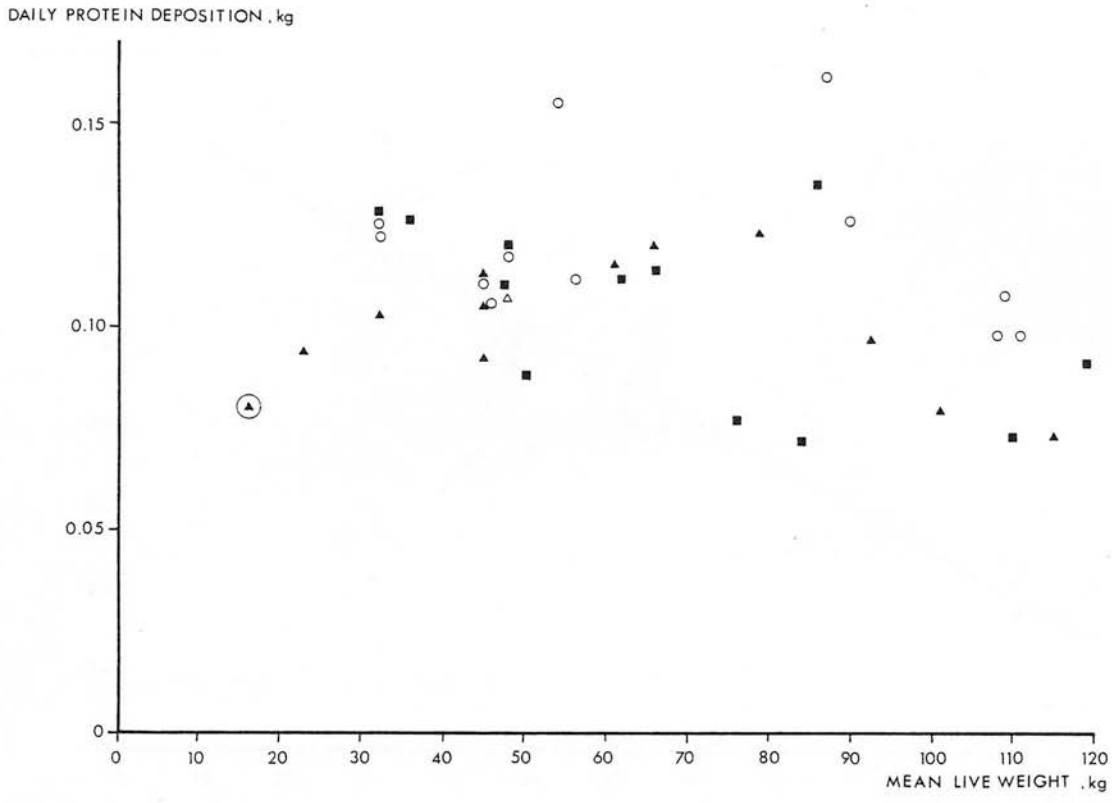


FIGURE 1.16: Daily protein deposition rate (kg) against mean live weight (between 20 kg and slaughter) for boars, gilts and castrates (n=36).

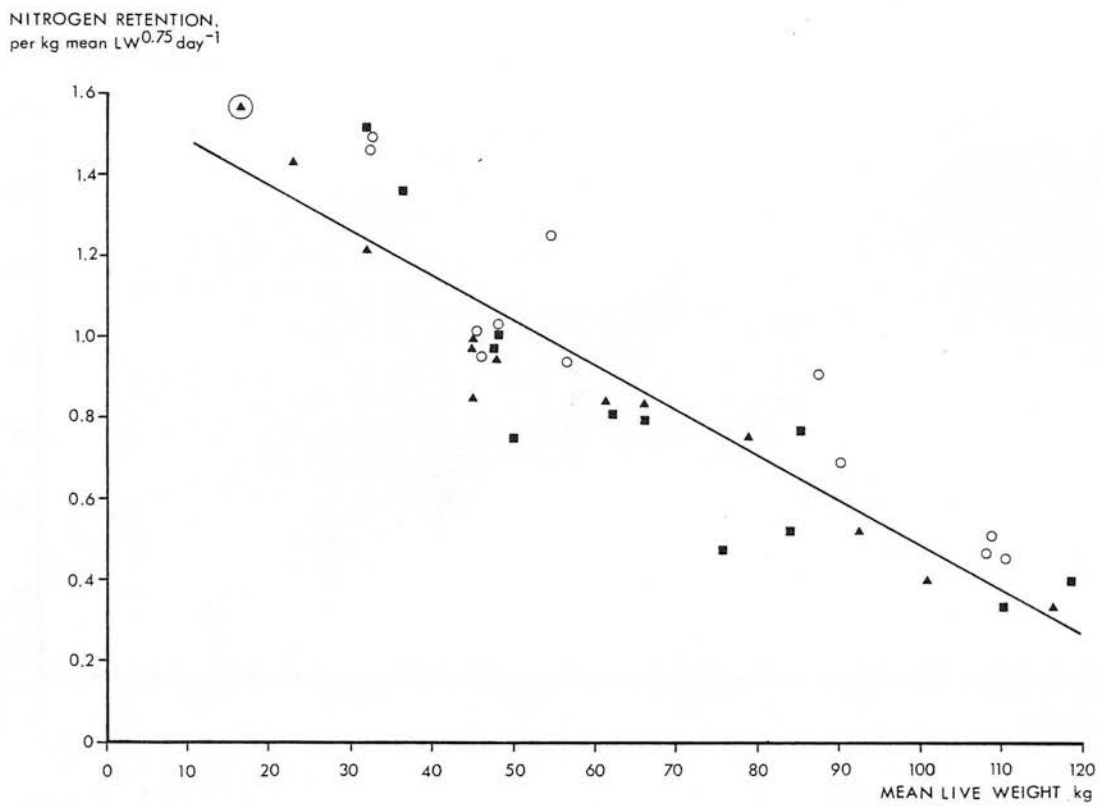


FIGURE 1.17: Daily nitrogen retention (g) per kg metabolic mean live weight by boars, gilts and castrates in relation to mean live weight (n=36).

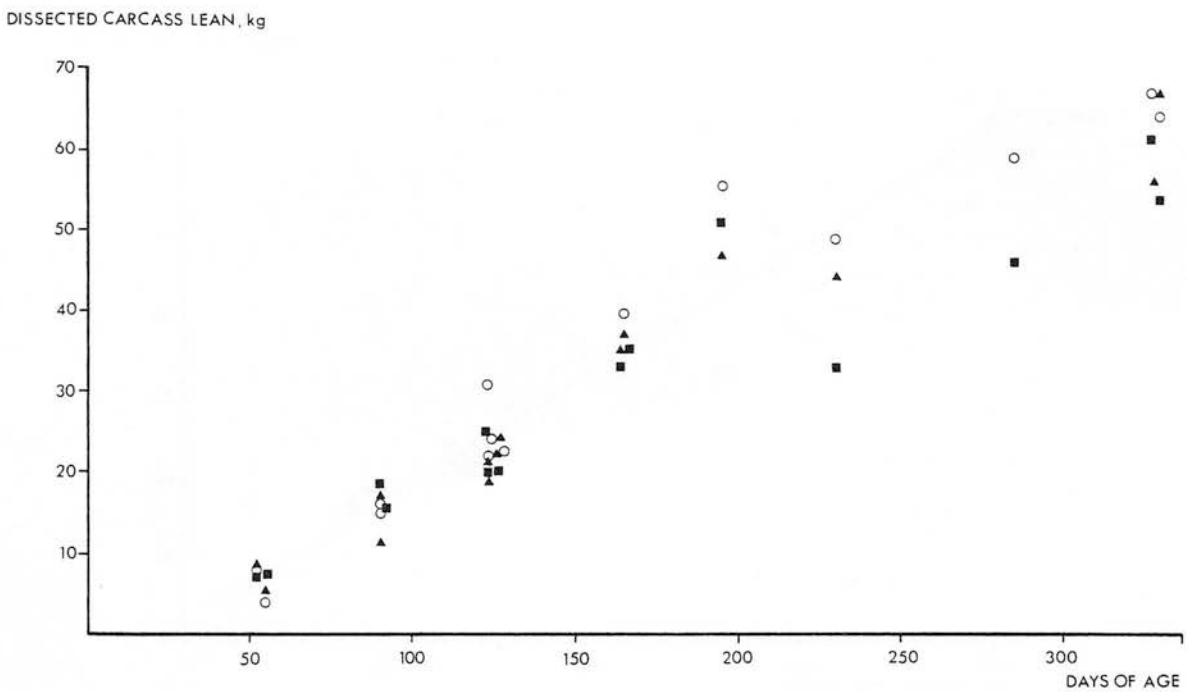


FIGURE 1.18: Dissected carcass lean (kg) as a function of age for boars, gilts and castrates (n=42).

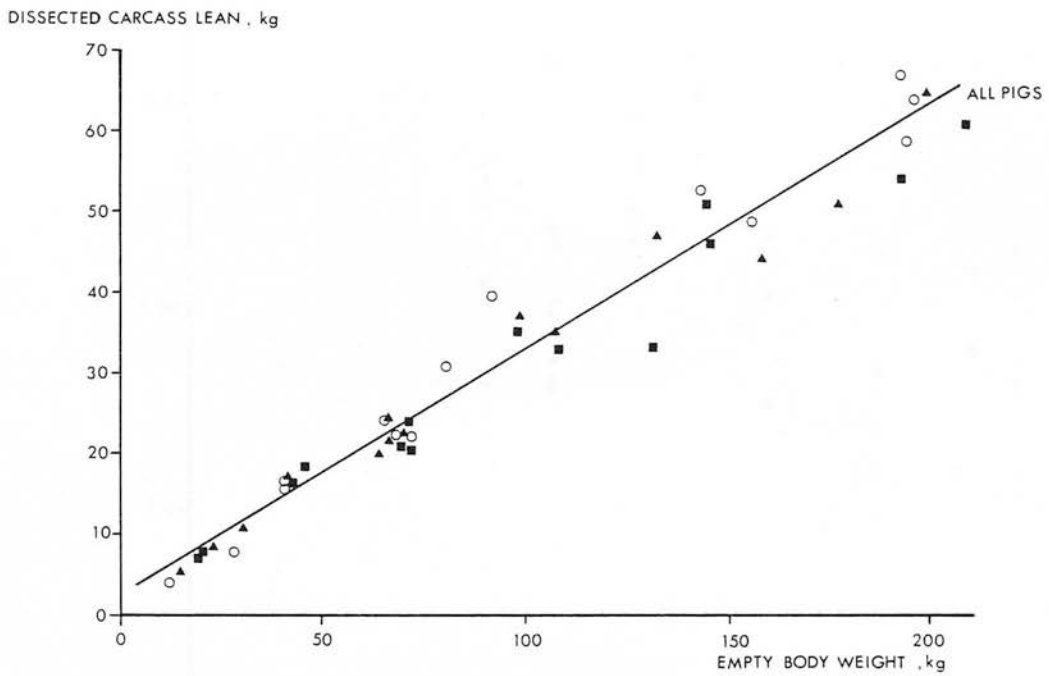


FIGURE 1.19: Dissected carcass lean (kg) as a function of empty body weight (kg) for boars, gilts and castrates (n=42).

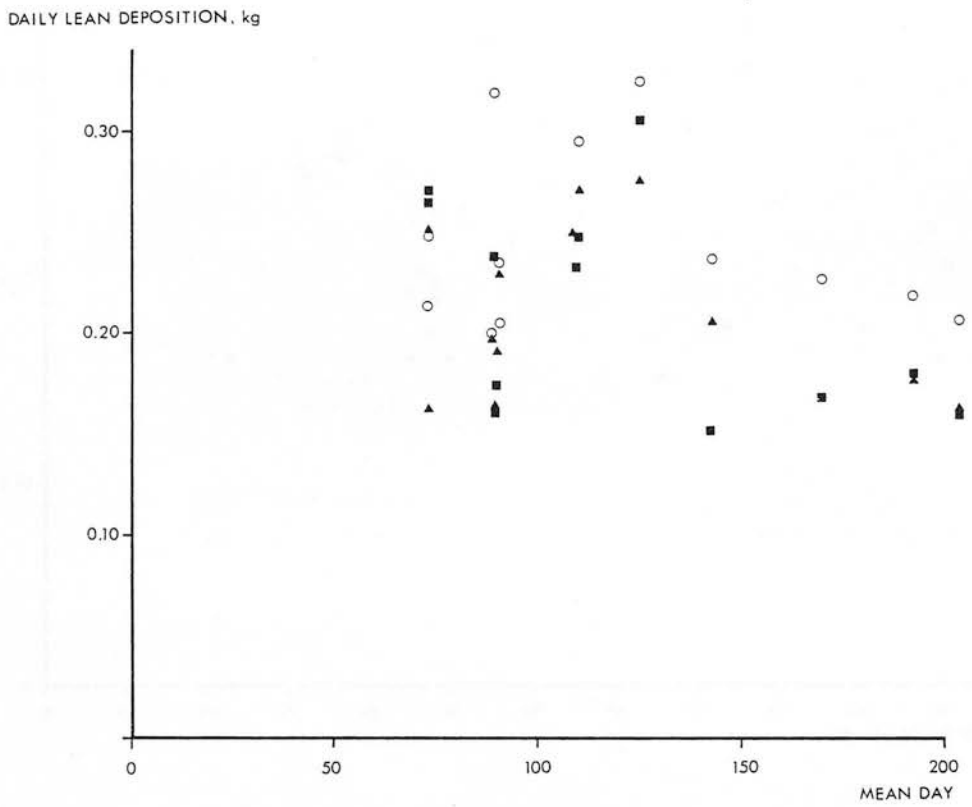


FIGURE 1.20: Daily lean deposition rate against mean day for boars, gilts and castrates (n=36).

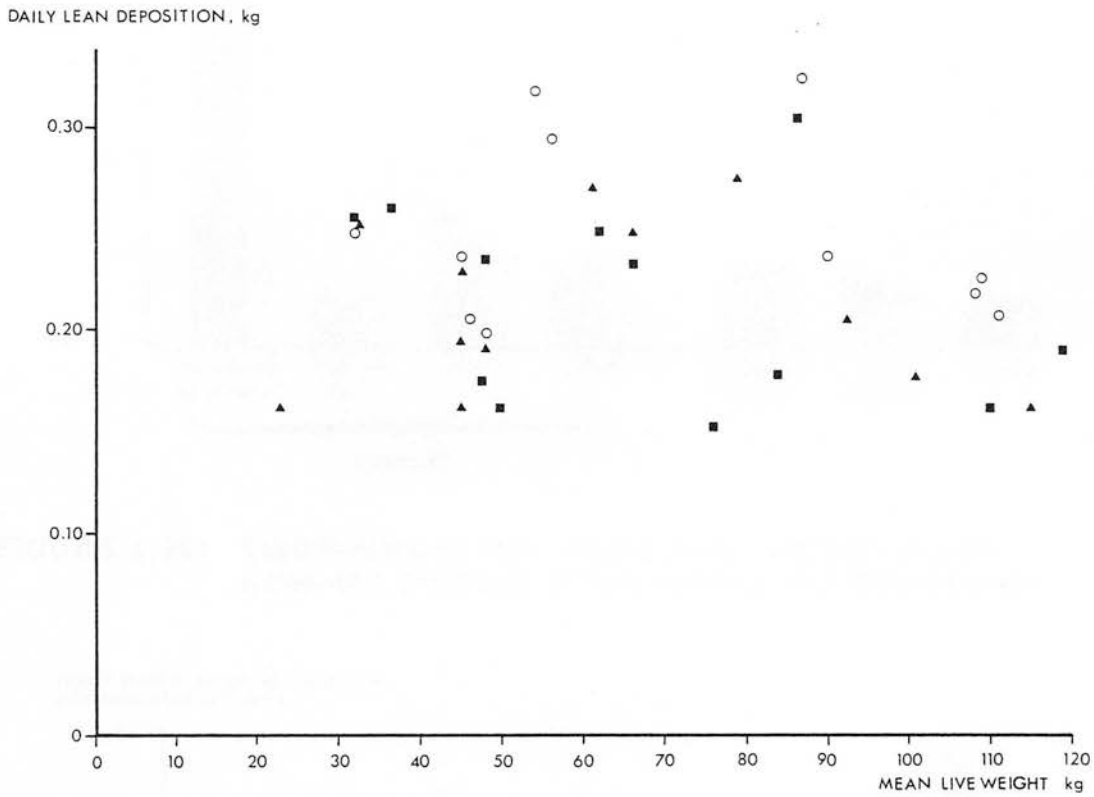


FIGURE 1.21: Daily lean deposition rate against mean live weight for boars, gilts and castrates.

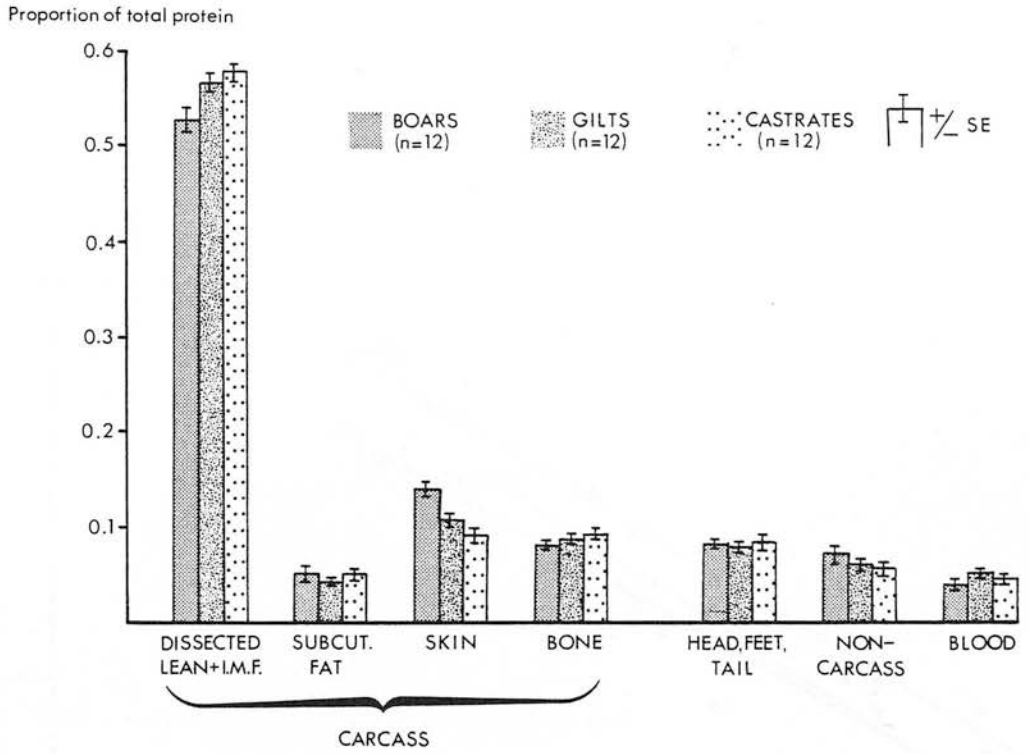


FIGURE 1.22: Distribution of total empty body protein between dissected fractions of the carcass and non-carcass.

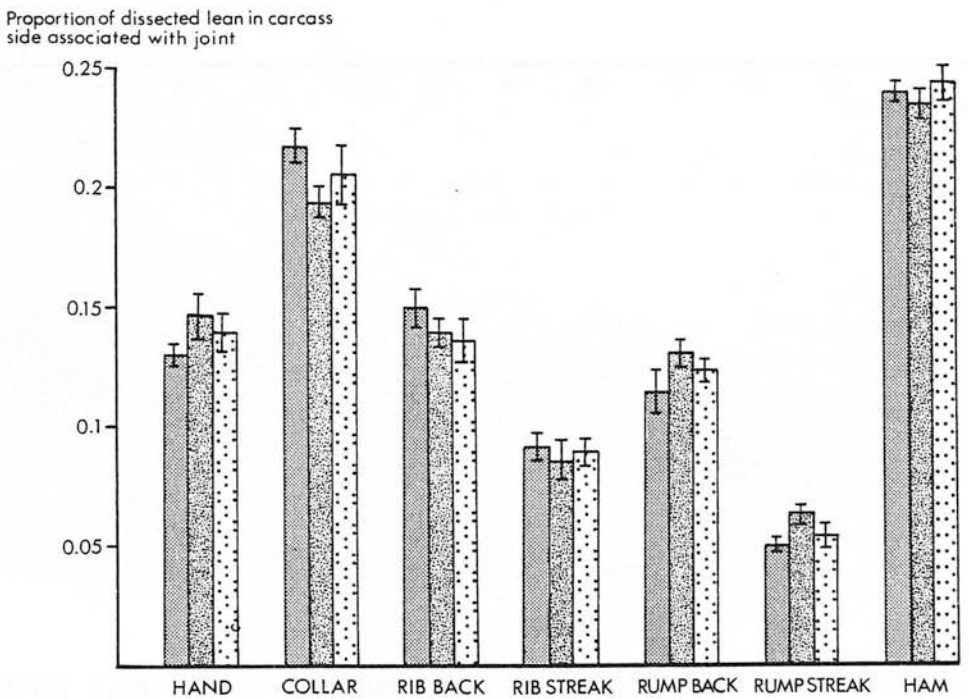


FIGURE 1.23: Distribution of dissected lean between standardised joints in the left carcass side.

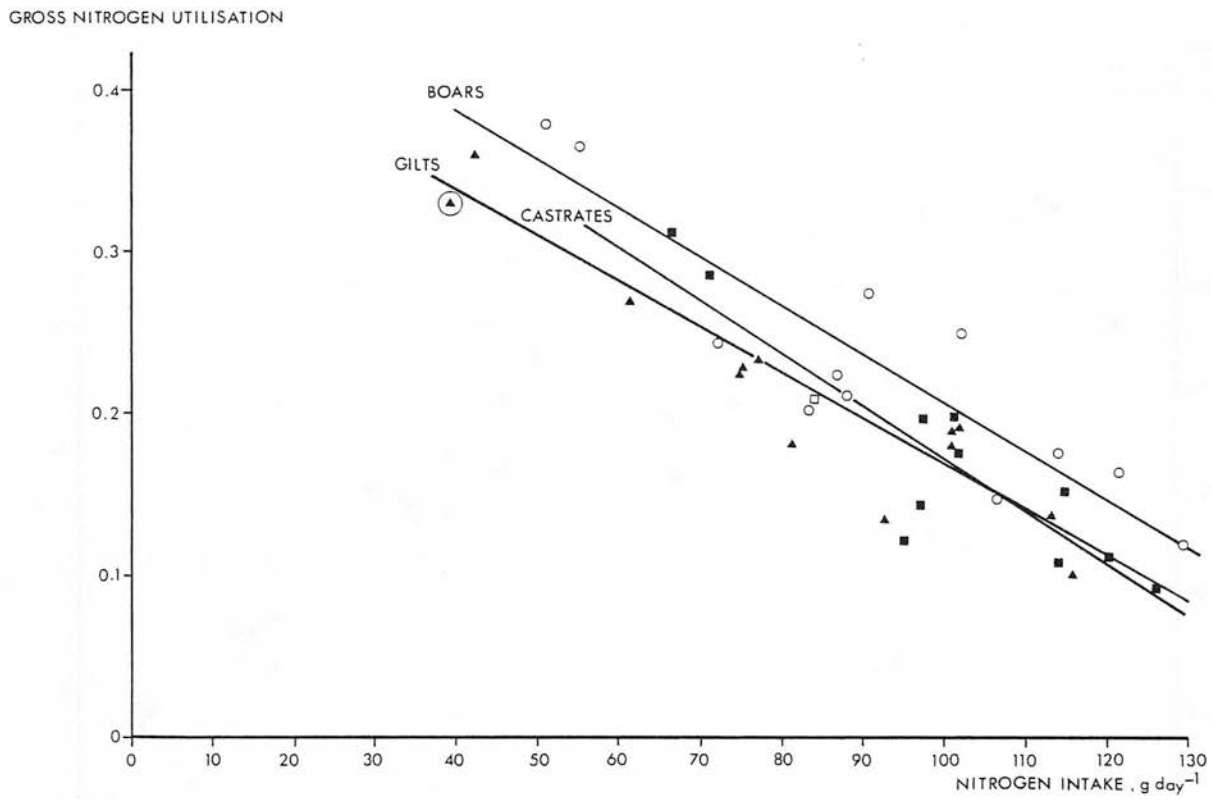


FIGURE 1.24: Gross nitrogen utilisation (nitrogen retained day^{-1} ÷ nitrogen consumed day^{-1}) against nitrogen intake (g day^{-1}) for boars, gilts and castrates (n=36).

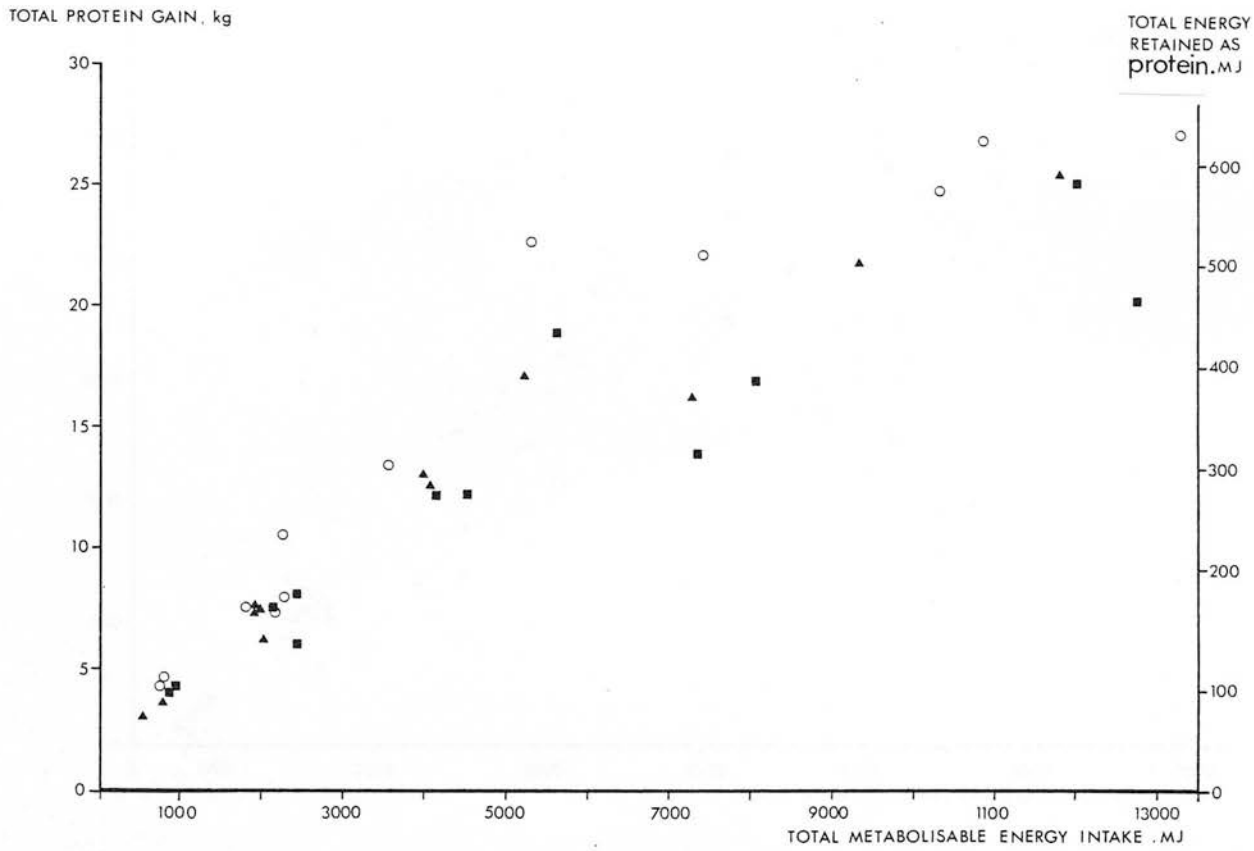


FIGURE 1.25: Total protein gain (kg) and total energy retained as protein (MJ) against total metabolisable energy intake (MJ) for boars, gilts and castrates (n=36).

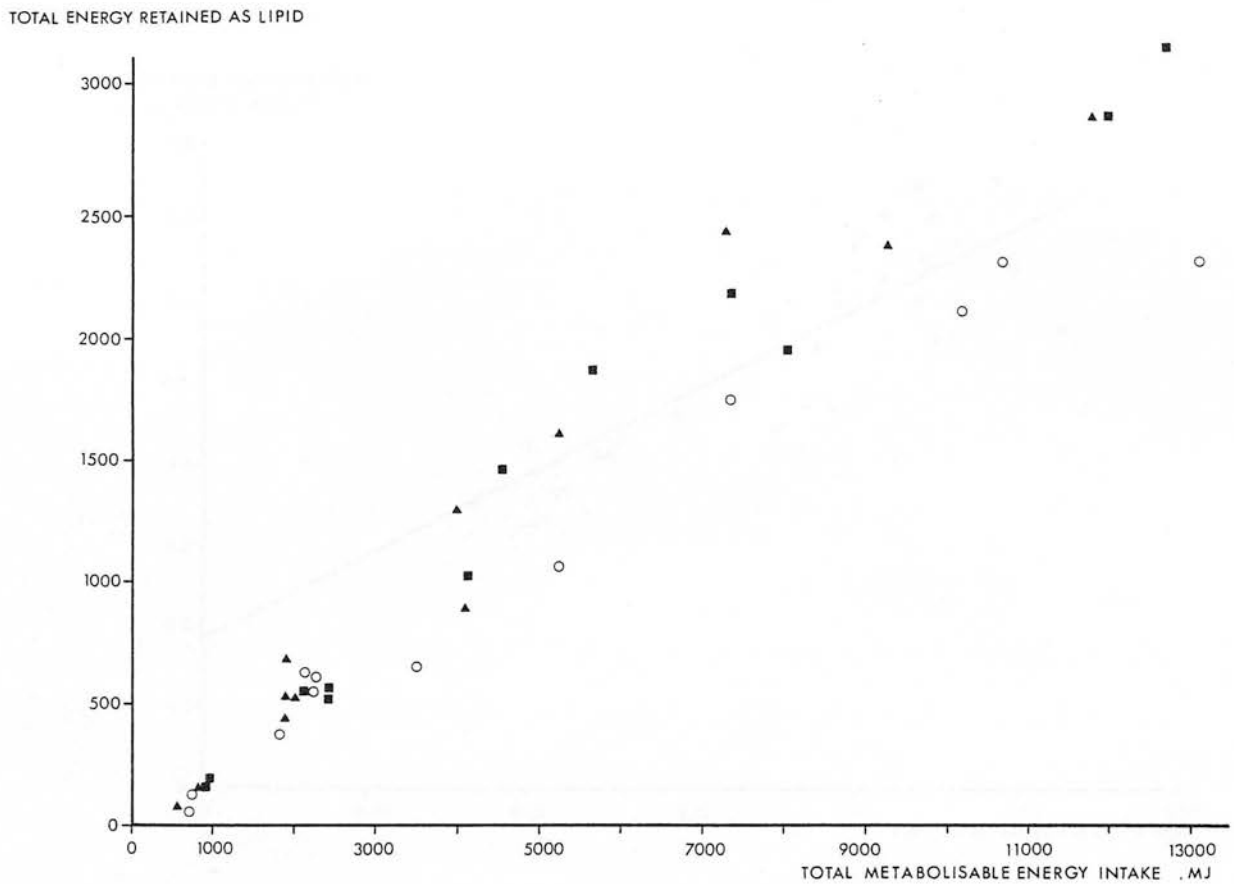


FIGURE 1.26: Energy retained as lipid (MJ) as a function of total metabolisable energy intake (MJ) for boars, gilts and castrates (n=36).

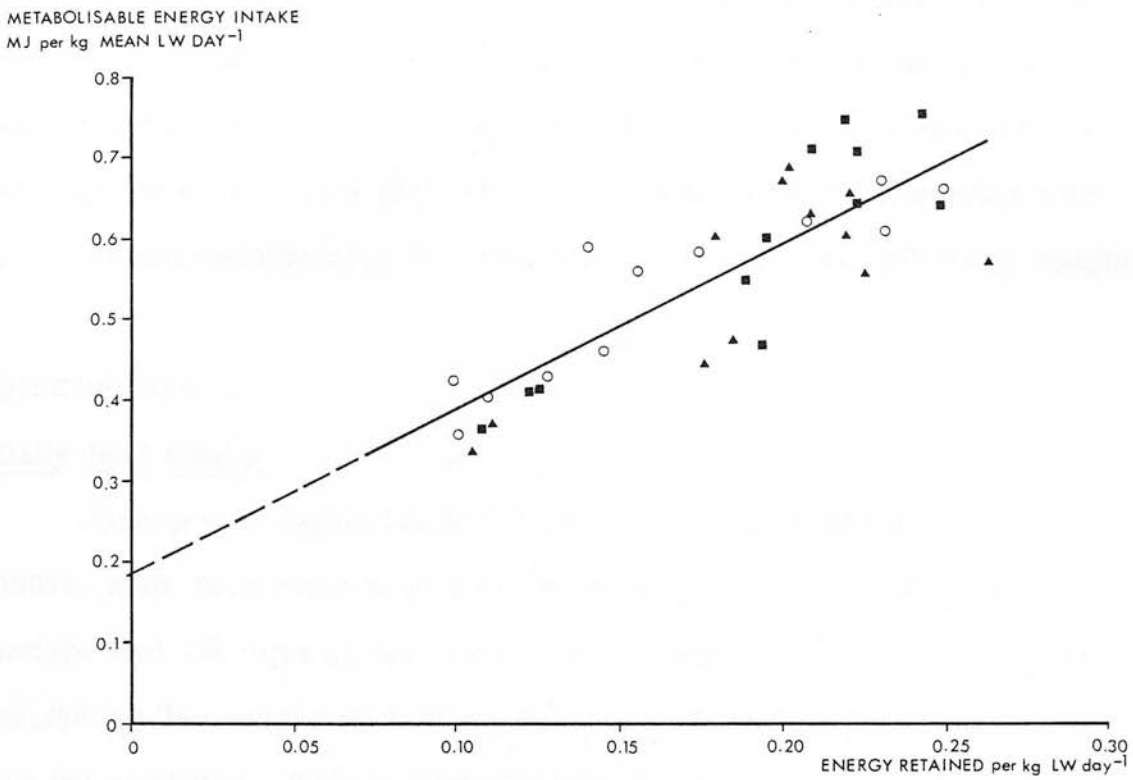


FIGURE 1.27: Daily intake of metabolisable energy per kg mean live weight as a function of daily energy retained per kg mean live weight.

At zero energy retention, MEI = 0.187 MJ per kg mean LW day^{-1}.

values for energy costs of tissue deposition are 69.0 MJ ME per kg protein and 56.0 MJ ME per kg lipid.

With the exception of protein mass for boars, the most appropriate basis on which to calculate ME_M, k_p and k_l for pigs of different sexes proved to be per kg live weight day^{-1}. Irrespective of method of calculation, boars and gilts required similar quantities of metabolisable energy for maintenance per unit body weight, whereas castrated male pigs needed considerably less maintenance energy per unit body weight.

DISCUSSION

Daily feed intake

Contrary to conventional wisdom (Cole, Duckworth and Holmes, 1967), daily feed intakes on appetite feeding were linear to 85 kg live weight and 140 days of age, and constant from 140 days until 330 days or 200 kg live weight at 3.97 kg for boars, 3.63 kg for gilts and 3.74 kg for castrates. This pattern of daily feed intake resulted in higher daily intakes than are suggested by a curvilinear function for intake relative to age or live weight, and this became more exaggerated with age. Castrated male pigs, 5 to 85 kg live weight, ate 0.12 more than boars and 0.15 more than gilts, similar differences to those cited by Fowler, McWilliam and Aitken (1981). Peak daily feed intakes were around 4.5 kg day^{-1} (supplying 58 MJ ME and 802 g DCP day^{-1}), which exceed voluntary feed intakes of 3.30 to 3.45 kg high-energy diet by boars, gilts and castrates of similar live weight (90 kg, Cole and Sparkes, unpublished). Average daily feed intake for all three sexes between 20 and 85 kg live weight was 2.40 kg; over the weight range 30 to 90 kg, Fowler *et al* (1981) found an average daily intake for boars, gilts and castrates of 2.66 kg high-energy diet. Vangen (1977)

recorded maximum daily feed intakes at 160 days of age and around 90 kg live weight in pigs fed to appetite on a fairly high protein diet (0.15 DCP); Headley (1961) observed peak feed intakes of 3.4 kg day^{-1} at 97 kg live weight and 168 days of age. The concensus, therefore, from this and other trials is that the highest daily feed intakes occur at 150-160 days of age and 85-95 kg live weight, when pigs will be approximately 0.40 of mature weight. The exception is to be found in the results of Kemm (1980): castrated male pigs fed *ad-libitum* on a 0.20 CP diet had a peak feed intake of 2.29 kg day^{-1} at 73 kg live weight and 157 days of age. Daily liveweight gains reached maximum rather earlier (125 days of age) and averaged at 0.645 kg; these figures suggest that the strain of pig used was of low weight for age (growth potential), and as such, may have been an early-maturing type of lower mature weight (for example 180 kg), whose maximisation of daily feed intake at 70 kg live weight was in keeping with the achievement of peak intake at 0.40 of mature size.

Daily feed intakes by growing broilers followed a very similar pattern to that of the boars illustrated in Figure 1.3: daily intakes rose linearly to a peak at 112 days of age (approximately 0.50 of maturity), and were then reduced to a mean value, about which there was considerable variation (Emmans, Parks, Wilson and Fawcett, 1975). Houseman, McDonald, Crofts and Fowler (unpublished) observed variation of up to 0.25 in weekly feed intake by individual pigs in the liveweight range 25 to 120 kg; a connection has been established, for younger pigs at least, between palatability of the diet and voluntary feed intake (Holub, 1969).

Voluntary feed intakes on the present trial were of sufficient magnitude that there is little reason to suspect a constraint on protein

and lean deposition rate by pigs in the live weight range studied (20-200 kg), even at the lower end of the live weight range. Thorbek (1975) suggested a daily intake for maximum protein deposition at 20 kg live weight of 125 g DCP and 12.0 MJ ME, while Carr *et al* (1977) proposed a daily intake of 214 g DCP and 16.1 MJ ME for maximum nitrogen retention at the same body weight. Intakes achieved by boars, gilts and castrates of 20 kg live weight were 226, 227 and 245 g DCP and 15.3, 15.4 and 16.6 MJ ME per day respectively. Just (1976) could not discern a clear correlation between increase in daily intake of DCP and ME and amount of protein deposited for castrated male and female pigs of 20 to 90 kg live weight, although if the assumption that intake limits protein deposition in young pigs is valid, then most of the potential response would occur at live weights of less than 20 kg. Similarly, Cöp (1974) found protein deposition rate to be independent of ME intake. Both these experiments seem to have fed sufficient energy for the achievement of plateau protein gains; until the latter is reached, there will be a potential response to additional ME intake. Claims to increase in daily deposition above plateau levels consequent upon a rise in ME intake (Clausen, Nørtoft Thomson, Christense and Danielsen, 1971) are suspect on the grounds that the contribution of intermuscular and intramuscular fat to lean weights will increase with ME intake under these circumstances. Eggum (1973) suggested that protein gains were not affected by the biological value of the protein source, provided that protein supply *per se* was adequate. Conversely, Sparkes, Cole and Lewis (1981) showed an improvement in both growth rate and % lean in the ham joint for increasing lysine concentration (and hence, biological value) of the diet; the inflection point in this response varied with sex of pig: 1.03, 1.19 and 1.03%

lysine in diet for boars, gilts and castrates respectively. The grower diet offered in the present experiment contained 0.0124 lysine. For the pigs fed to appetite on a single diet (containing 178 g DCP kg^{-1}) from 50 to 330 days of age, excess protein supply at higher live weights may have somewhat curtailed lipid deposition, energy being required for deamination of surplus protein.

Of future interest would be the measurement of daily feed intake beyond the final slaughter age used in this experiment to examine the time period over which the mean feed intakes observed between 140 and 330 days of age (3.97, 3.63, 3.74 for boars, gilts and castrates) were sustained. Gilts in particular showed signs of a gradual reduction in mean daily feed intake from 250 days of age.

Characteristics of daily protein and lean deposition rate

In examining the influences of age, sex, genotype (strain of Large White) and feed intake on daily protein and lean deposition rate, this experiment has confirmed the stability of protein content of the empty body over a very wide range in empty body weights, namely, 0.144 for boars and gilts and 0.124 for castrates. Also established by this study was the invariability of dissected lean as a proportion of empty body weight: 0.305 for all sexes. The relationship between dissected lean mass and total body protein mass was 2.21, again with no significant variation between sexes of pig.

Within the liveweight range covered (20 to 200 kg), no positive correlation was produced between daily feed (protein) intake and daily protein and lean gains. There are two possible explanations for this result: first, pigs had reached the stage by 20 kg live weight where protein accretion was no longer constrained by appetite or second, curtailment of protein gains by feed intake was sufficiently small to

have been concealed within the overall gains for the period of measurement. If either of these explanations pertain, then the effect of intake limitation on daily protein gain should have been evident during the first measurement period, 55 to 91 days of age or 20 to 45 kg live weight. Values in Table 1.7 for daily protein gain over the period appear to refute this premise as daily protein deposition rates were considerable. Measured deposition rates between 20 and 45 kg live weight, particularly those of boars and castrates, exceeded the values predicted for pigs of the same body weight by Thorbek's equation (1975), the function given by Carr *et al* (1977) and by a combination of the Gompertz function and allometry. Predicted values were similar to, or rather better than, measured protein gains over the next period, 55 to 125 days of age and 20 to 75 kg live weight. However, as noted previously, the trios of pigs slaughtered at 125 days had a lower than average protein growth performance. Predicted daily protein gains accorded reasonably well with measured values for the period 55 to 165 days, 20 to 105 kg live weight, with the exception of castrated male pigs whose actual performance surpassed all estimations of protein deposition rate.

Where predictions clearly depart from observed values is in their estimated velocity of decline in daily protein deposition rate from 100 kg live weight. Measured protein gains between 55 and 231 days of age, 20 to 150 kg live weight, point to high daily protein deposition rates being sustained for longer in practice than predictive functions take into account; acknowledging the disproportionate contribution to the mean of pigs from litter 11, when total protein gained is averaged over 176 days (55 to 231 days) the values obtained are still well in excess of 100 g day^{-1}.

TABLE 1.7: Predicted and measured daily protein deposition rate (g)

Live weight (kg)	Thorbek[1] (1975)	Carr *et al*[2] (1977)	Present trial[3] - predicted			Liveweight range	Present trial[4] - measured		
			boars	gilts	castrates		boars	gilts	castrates
10		86	51	55	54				
20	72	104	77	80	75				
30	91	103	95	96	88	20-45 (n=6)	124	98	127
40	105	100	108	107	96				
50	115	106	116	113	101	20-75 (n=11)	122	104	106
60	122	110	122	117	103				
70	126	112	125	118	103	20-105 (n=5)	122	117	113
80	128	110	126	117	102				
90	128	106	126	114	100	20-150 (n=6)	144	110	106
100		99	123	109	96				
110		89	119	103	91	20-200 (n=8)	101	83	79
120		77	114	96	85				
130		62	108	88	79				
140		46	101	79	72				
150		26	93	69	64				
160			83	58	56				
170			73	46	47				

[1]NR (g day^{-1}) = 1.479 $kgW^{0.75}$ - 0.0266 $kgW^{1.50}$ 20-84 kg live weight.

[2]NR (g per $kgW^{0.75}day^{-1}$) = 3.324 - 0.098 W + 0.001 Z.

[3]Gompertz and allometry.

[4]Δ P, 55 days to slaughter ÷ days on test.

It seems reasonable to conclude from this comparison of predicted and measured daily protein gains that the functions of Thorbek (1975) and Carr *et al* (1977) tend to underestimate daily protein deposition rate in young pigs and pigs weighing more than the usual slaughter weights. Significantly, measured values substantiate the proposal (represented by the fine solid line in Figure 1.1) that young pigs, if persuaded to consume more food, can achieve greater daily protein gains than their ages and live weights would have hitherto suggested. There was no evidence that early accomplishment of maximum daily protein gain was associated with a premature decline in protein and lean deposition rate.

The overall shape to daily protein growth probably lies between the two shapes illustrated in Figure 1.1. It is naive to suppose that maximum daily protein deposition rate could be maintained as a constant between 5 and 150 kg live weight. Nevertheless, the quadratic function describing a peak in daily deposition rate at around 60-80 kg live weight and similar rates of ascent to peak gain and descent from peak gain has also been challenged. If in essence quadratic, then the pattern to daily gain was more appropriately delineated by the 'skewed' quadratic produced by combination of the Gompertz function and allometry: this traces a rapid increase in deposition rate by young pigs approaching maximum daily protein gain, a relatively flat peak, and gradual decline in deposition rate at heavier live weights.

Averaging the daily protein gains given in Table 1.6 for the period of measurement over which there was little change in deposition rate, that is, 55 to 195 days of age and 20 to 150 kg live weight, protein deposition rate was 0.128 kg day^{-1} for boars, 0.108 kg day^{-1} for gilts and 0.117 kg day^{-1} for castrates. Corresponding values for

average daily lean gains, 20 to 150 kg live weight, were 0.255, 0.221 and 0.234 kg for boars, gilts and castrates respectively. It is not suggested that these represent maximum daily protein and lean gains for a majority of pigs but that they indicate maxima for pigs of average protein and lean growth potential in response to the conditions under which they were measured. The highest gains obtained were those of the entire male from litter 11 who deposited 0.162 kg protein and 0.324 kg lean per day between 20 and 150 kg live weight (55 to 195 days of age).

Extrapolation of measured protein masses at slaughter to protein mass at maturity assess the latter as 36 kg for boars, 29 kg for gilts and 30 kg for castrates. There are no figures of protein mass at maturity to be found in the literature; tentative suggestions, based on a few Polish pigs, are 30 to 35 kg for gilts and castrates and 50 kg for boars (Polish data, unpublished). A degree of concurrence for females and castrate males' protein mass at maturity does not extend to suggested values for boars, which the present trial estimates to contain considerably less than 50 kg protein when mature.

Dissected lean weights relative to body weights were similar to other published values for *ad-libitum* fed pigs between 20 and 65 kg live weight, but were rather lower than other values at heavier body weights, particularly where dissected lean weights apply to selected pigs (Stant, Martin, Judge and Harrington, 1968; Harbison, Darrel, Goll, Parrish, Wang and Kline, 1976; Evans and Kempster, 1979). While admitting that the pigs used in this experiment were not of outstanding genetic merit, it is difficult to compare dissected lean weights between trials when the degree of accuracy in separating carcass lean from carcass fat is not discernable. Average daily lean tissue gains

by breeding company gilts and castrates in years 1-4 of the MLC's Commercial Product Evaluation were 0.299, 0.305 and 0.294 kg over the periods 27-61, 27-91 and 27-118 kg live weight (MLC, 1978).

The outcome of selection for protein and lean growth should be that selected pigs show the protein and lean growth characteristics of entire males (later-maturing pigs), that is, superiority of gains at higher live weights (boars tending to have lower voluntary food intakes early on in the growth phase) and prolongation of the period over which maximum daily gains are sustained. Administration of androgens to female rats, to investigate the endocrine balance responsible for the advantage of male animals in protein growth potential, brought about a slight reduction in overall level of protein synthesis in conjunction with the deposition of a larger proportion of the quantity of protein synthesised (Vernon and Buttery, 1978). Entire males in this experment deposited significantly less protein in the dissected lean plus intermuscular fat fraction and significantly more protein in the skin than females or castrated males ($P < 0.05$); this may be connected with their relative vulnerability under circumstances of protein shortage and their consequent requirement to "store" protein in labile reserves such as the skin or viscera instead of skeletal muscle which is afforded some measure of protection from mobilisation when protein intake is low (see Section III).

The decrease in efficiency of protein utilisation (GNU, Figure 1.24) with age and live weight was to be expected for pigs fed to appetite over so long a period, and followed the pattern outlined by Carr *et al* (1977). The more pronounced decline in GNU with live weight for gilts and castrates is indicative of greater deamination of surplus protein by animals of lower daily protein growth potential.

There was a clear relationship between daily protein deposition rate and daily lean deposition rate ($r = 0.86$), indicating that improvement in one of these would be accompanied by progress in the other. The connection between daily protein gain and daily liveweight gain was rather less positive ($r = 0.71$). Duniec, Kielanowski and Osińska (1968), reporting the testing of pigs on a fixed feed, fixed time trial, found a correlation of 0.87 between daily protein deposition rate and daily liveweight gain. The latter has a reasonably high heritability, suggesting some scope for improvement in daily protein gain by selection. The inclusion of daily liveweight gain in a selection index with a view to indirect progress in protein deposition rate, as opposed to direct selection of pigs showing more rapid protein or lean gains, should be limited to pigs which are not prone to excessive fat deposition. Unless selection on the basis of daily liveweight gain is confined to pigs with low lipid : protein ratio in the daily gain, then increase in liveweight gain will be linked to considerable daily lipid accretion. In this trial the highest daily rate of protein deposition, 162 g, was measured in an entire male between 55 and 195 days of age, 20 to 150 kg live weight, and was associated with an overall lipid : protein ratio of 1.22 : 1 over the wide age and liveweight range. If 1.22 : 1 was the achieved lipid : protein ratio in the liveweight increment, then the minimum ratio in this boar's gain must have been considerably lower than 1 : 1. An appropriate selection policy for the improvement of daily protein and lean gains should avoid discrimination in favour of pigs which partition energy to heat loss or fat gain, the former because slow growth is energetically inefficient and the latter because it would depreciate carcass value. Fowler (1978) proposed that the most important contribution to improving efficiency of energy utilisation would come from

increase in daily lean tissue gain; for pigs which have been subject to selection for low backfat depth, and have reduced voluntary feed intakes as a result, selection may also have to concentrate attention on appetite if potential daily protein and lean deposition rates are to be achieved.

Distribution of dissected carcass lean between standardised joints

Lean mass distribution in pig carcasses has been shown to be relatively stable, both genetically and environmentally (McMeekan, 1940; Richmond and Berg, 1971). However, slight genetic differences in lean weight location in the carcass were detected on analysis of CPE data (Kempster and Evans, 1979a) and in the comparison of Duroc x Yorkshire with Hampshire x Yorkshire pigs (Richmond and Berg, 1971), these differences being attributable to discrepancies in degree of maturity at time of slaughter (Davies, 1974). Apart from certain secondary sexual characteristics such as development of neck muscles in the entire male at higher live weights (which resulted in a significantly ($P < 0.05$) higher proportion of dissected lean in the collar joints of boars than in those of females), differences between sexes in lean distribution are linked to differences in relative maturities of muscle groups. Richmond and Berg (1971) found gilt carcasses to contain relatively more lean in proximal limb joints (low relative growth rate) and relatively less lean in abdominal and spinal joints (high relative growth rate) than carcasses of castrated males. This suggests that the female is rather later-maturing than the castrated male. Failure of the present experiment to detect significant differences in lean weight distribution between these two sexes is probably due to the wide range in carcass weights and inclusion of fairly mature pigs in the analysis, which would tend to mask any variation in degree of muscle

development apparent at commercial slaughter weights. However, rump streak joints from boar carcasses did contain significantly less lean than rump streak joints from gilt carcass ($P < 0.05$), inferring that the abdominal muscles are later-maturing in entire males than in females.

Backfat depth in relation to carcass lean content

Adoption of backfat depth measurement in the region of the hind rib stemmed from the suggestion by Hammond (1933) and McMeekan (1941) that the junction of loin and thorax is the best region for prediction purposes since it is the latest-developing part of the carcass. Kempster and Evans (1979b) found the most precise predictions of carcass lean percentage in pigs of different sexes, genotypes and slaughter weights (MLC, 1975 and 1976) to be provided by optical probe measurements at the P2 position and at the 13th rib. Only very slight improvement in accuracy was achieved by deriving different relationships between P2 and % carcass lean for gilts and castrated males. This procedure may be of greater benefit where boar carcasses are to be compared to the other two sexes (Buck, Harrington and Johnson, 1962), although no significant differences between sexes were detected in the present experiment and a single equation sufficed for boars, gilts and castrates (% carcass lean = 61.22 - 0.494 P2 (cold, mm)). Kempster and Evans (1979b) used CPE data to generate the following:

Pork weight	% carcass lean = 59.88-0.733 P2 (hot, mm)
Bacon weight	% carcass lean = 59.52-0.633 P2 (hot, mm)
Heavy weight	% carcass lean = 57.40-0.543 P2 (hot, mm)

Cold P2 measurements, generally larger than hot P2 measurements, tend to give a rather better prediction of carcass lean content. Although not derived from carcasses in the same weight range, comparison of predicted P2 values at a particular % carcass lean, for example, 49%,

indicates that the appetite-fed pigs on the present trial would have a very much greater depth of backfat than MLC bacon carcasses (24.7 vs 16.6 mm at P2). This difference is greater than anticipated, bearing in mind that roughly 0.5 of the CPE animals used to produce the Kempster and Evans (1979b) equations had been fed *ad-libitum*. There must have been a feed level : genotype interaction, with breeding company pigs selected for lower propensity for fatness having lower appetites or higher maintenance requirements to account for their lower P2 backfat depths. The possibility of a relocation of fat deposition within the body by selected animals (for example, preferential fat accretion in non-carcass fat depots relative to the subcutaneous fat depot) was discounted by the findings of Henderson, Whittemore, Ellis, Smith and Laird (1980) with the Newcastle Large White selection line. For pigs grown on a restricted daily intake, females have more carcass lean than castrates at an equal P2 backfat measurement (Kempster and Evans, 1979b).

Energy requirement for maintenance

Energy requirement for maintenance (ME_M) is a compilation of the energy costs of basal metabolism, maintaining body temperature, locomotion and the work of digestion (Kielanowski, 1966). Of these, basal metabolism makes by far the greatest demands on available energy. Of the two estimates of ME_M calculated for pigs in the present trial, 0.535 and 0.545 MJ ME per $kgW^{0.75}$ day^{-1} (derived by extrapolation to zero energy retention and multiple regression respectively), the second is the preferred estimate as it avoids the problems of fat mobilisation at zero energy retention concurrent with nitrogen retentions of 3-7 g day^{-1} (30-60 kg live weight: Fuller, Webster, MacPherson and Smith, 1976; Close, Mount and Brown, 1978).

The appropriate exponent for the expression of fasting heat loss and maintenance energy requirement has been the subject of debate. Brierem (1939) found 0.56 to be the most suitable exponent for pigs of 6 to 169 kg live weight used in starvation trials. Balance experiments with pigs of 20-90 kg live weight produced a very similar exponent, 0.57 (Fuller and Boyne, 1972), while Mount and Rowell (1960) obtained a value of 0.56 from their experiments with pigs of 70 kg and above. Verstegen (1971) suggested that $W^{0.55}$ be used for pigs weighing more than 50 kg. For younger pigs, exponents of 0.73 (Mount and Rowell, 1960), 0.734 (Kielanowski and Kotarbińska, 1970) and 0.85 (Verstegen, 1971) have been proposed; only the last of these is significantly different from 0.75 (Kielanowski, 1976). The convention of adopting 0.75 as the exponent over an entire weight range, and reflecting differences between animals by the coefficient, has been followed in this experiment. However, Fowler, Fuller, Close and Whittemore (1980) were in favour of using $W^{0.66}$ for pigs weighing between 2 and 110 kg live weight.

Estimates of energy requirements for maintenance derived by multiple regression are given in Table 1.8. In general, ME_M requirement proceeds inversely to live weight. Fowler *et al* (1980) put the rate of decline in ME_M at 1.48 kJ per $kgW^{0.75}$ day^{-1} for each kg increase in body weight between 5 and 90 kg, while Berschauer *et al* (1980) proposed 1.59 kJ per kg $W^{0.75}$ day^{-1} per kg live weight gained between 40 and 110 kg live weight. In corroboration of this trend, Thorbek (1974) measured a negative gradient in heat production with age and weight: raised to the power $W^{0.903}$, coefficients were 63.5 (kJ) for pigs of 25-30 kg, 37.7 for the range 50-80 kg and 38.8 at 95-100 kg live weight. The value of 0.545 MJ ME per $kgW^{0.75}$ day^{-1} for maintenance

TABLE 1.8: Estimates of energy requirement for maintenance (ME_M) and efficiencies of energy utilisation for protein and lipid accretion (k_p and k_l) from multiple regression equations.

Live weight (kg)	Sex	n	Method[1]	ME_M per $kgW^{0.75}$ ($MJ\ day^{-1}$)	k_p	k_l	Reference
6	B,G,C	18	S,C	0.554[2]	0.74	0.72	Close and Stanier (1980)
5-40	C	36	ENB	0.510	0.66	0.73	Halter, Wenk and Schürch (1980)
20-40	C	28	ENB,C	0.511	0.57	0.69	Close, Verstegen and Mount (1973)
20-50				0.440	0.63	0.70	Close and Mount (1976)
20-90	G,C	273	S	0.418	0.35	0.73	Kotarbińska (1969)
20-90	C	24	S	0.429	0.37	0.91	Houseman and McDonald (1973)
30-110	ng	6	C	0.377-0.418	0.54	0.70	Gädeken, Oslage and Fliegel (1974)
32-104	B	122	S	0.466	0.32	0.68[3]	Walach-Janiak, Kotarbińska, Kielanowski (1980)
40-75	ng	8	ENB,C	0.497	0.57	0.91	Berschauer, Gaus and Menke (1980)
75-110	ng	8	ENB,C	0.453	0.60	0.82	
20-200	B,G,C	36	S	0.545	0.27	0.73	present trial

[1]Comparative slaughter (S), energy and nitrogen balance (ENB), calorimetry (C).

[2]Measured at thermoneutrality (28°C).

[3]Assume value.

ng, not given.

Boar (B), gilt (G), castrate (C).

energy requirements obtained in the present trial does not follow this pattern, and when considered in conjunction with the low estimate of k_p (0.27) suggests a low overall efficiency of energy utilisation. This need not detract from the credibility of these results: it is common for ME_M estimates accruing from slaughter trials to exceed those produced by energy and nitrogen balance and calorimetry studies. Although the former method estimates ME_M indirectly, it usually has the advantage of measuring efficiencies of energy utilisation over longer sections of the growth phase than the latter two methods, and in doing so may arrive at a more realistic assessment of energy utilisation for maintenance and protein deposition.

Higher ME_M in younger pigs is associated with higher efficiencies of energy retention (k_w). This connection may be indicative of the composition of tissues deposited in early post-natal life. Dramatic change in the composition of weight gain with age was demonstrated by the experiment of Rothwell, Stock, Gurr, Mawson and Fisher (1980): 6 kg pigs responded to a low protein-high energy diet by dissipating excess energy intake as heat, whereas 20 kg pigs fed the same diet directed 0.80 of excess energy into carcass fat deposition.

Sex of pig has also been shown to influence energy requirements for maintenance. The similarity in estimated ME_M requirement between boars and gilts (0.618 and 0.588 MJ ME per $kgW^{0.75}$ day^{-1}) and much lower value of ME_M obtained for castrates (0.448 MJ ME per $kgW^{0.75}$ day^{-1}) is in agreement with the findings of Fuller, Gordon and Aitken (1980), who could not detect differences in heat output of boars and gilts when adjusted to the same live weight but reported a significantly lower heat output by castrates. Ritzman and Colovos (1943) had previously established a difference in heat production relative to weight

between boars and castrates; heat output by bulls was found to be 0.20 higher than castrates at equal feed intakes and stages of maturity (Webster, Smith and Mollison, 1977). However, for a given daily ME intake per $kgW^{0.75}$, male chickens had a 0.17 higher heat output than female chickens (Chwalibog, Henckel and Thorbek, 1978) and required more maintenance energy daily (Guillaume, Derouet, Bellec and Gomez, 1976; Johnson and Crownover, 1976). Kotarbińska (1969) failed to establish a difference in ME_M between castrated males and gilts, and Fuller and Livingstone (1978) estimated lower ME_M values for gilts than for castrated males (0.380 vs 0.440 MJ ME per $kgW^{0.75}$ day^{-1}). Thus the more recent evidence supports the findings of this trial and results from earlier trials do not; these contradictions may stem from a failure, in earlier experiments, to take into account relative maturity.

Less equivocal is the explanation for higher ME_M requirements for animals of greater protein growth potential. Each increment of protein to the protein mass incurs a higher maintenance cost for upkeep of the mass, in addition to which, a faster rate of protein deposition is the end product of a greater volume of protein synthesised, and therefore, increased protein turnover and heat output. Boars have been shown to require more maintenance energy per unit metabolic weight than contemporary gilts and castrates (Table 1.8). By extrapolation, animals selected for leanness should also exhibit elevated ME_M requirements. This was certainly the case for lean and fatty Zucker rats: at the same live weight, lean rats needed 0.55 more energy per day for maintenance (Pullar and Webster, 1977). There was a close correlation between rate of protein synthesis and heat production in lean and fatty rats ($r = 0.90$), the correlations between body protein mass or body weight and heat production being considerably lower. It is the opinion of Webster,

Lobley, Reeds and Pullar (1978) that protein synthesis and those aspects of metabolism associated with it account for 0.50 of heat production, a much higher proportion than the 0.17 proposed for pigs by Garlick, Burk and Swick (1976). Sunstøl, Standal and Vangen (1979) found higher fasting metabolism in pigs selected for low backfat thickness and more rapid liveweight gain. Breeds of pig can likewise demonstrate genetic differences in ME_M. Sharma, Young and Smith (1971), estimating ME_M at zero energy retention, found a 0.25 higher energy maintenance requirement in relatively lean Yorkshire pigs compared with Lacombes (0.570 vs 0.455 MJ ME per $kgW^{0.75}\,day^{-1}$). Litters of Large White pigs in the present trial which produced the highest daily protein gains (litters 6 and 11) would have been expected to undergo a concomitant increase in ME_M requirement, had it been possible to assess ME_M for individuals.

A drawback to the selection of animals with greater voluntary feed intakes, on the grounds that these are most likely to attain maximum daily protein deposition, is that of picking animals which have a higher ME_M requirement relative to their weight (Webster, 1980).

Efficiencies of energy utilisation for protein and lipid deposition

The method of estimation of efficiency of energy utilisation for lipid accretion (k_l) has little influence on the value produced (Armstrong, 1969; Menke, 1975; Mount, 1980). Biochemical deductions predict k_l to be 0.80. Estimates generated by slaughter or respiration trials tend to fall within the range 0.70 to 0.80, which suggests that for continuous growth the ratio of lipid synthesised to lipid deposited does not differ radically from unity (Webster, 1980), that is, k_l is not age or weight dependent. Evidence suggests that there is some variation in k_l in response to different diet composition, with diets high in

triglyceride increasing the value of k_l to 0.87, while those containing more carbohydrate having a k_l value close to 0.71 (ARC/MRC Committee, 1974). Similarly, Thorbek (1975) found maize-based diets to lead to significantly greater efficiency of energy utilisation for lipid deposition than barley- or sorghum-based diets (0.83 vs 0.75). Increasing the protein content of a diet beyond certain limits will depress k_l (Close and Berschauer, 1980), presumably reflecting the energy cost of deamination. The k_l value estimated in the present trial, 0.73, was in good agreement with the general range of values in the literature (Table 1.8). By predicting the energy costs of lipid deposition to be 54 MJ ME per kg lipid deposited, the results produced by pigs ranging from 20 to 200 kg live weight concur exactly with those of Kielanowski (1972), and Pullar and Webster (1977) for rats.

From biochemical deductions as to energy expenditure for protein synthesis, the efficiency of energy utilisation for protein deposition (k_p) should be around 0.76 (Armstrong, 1969; Kielanowski, 1972) and the energy cost of protein deposition approximately 31 MJ ME kg^{-1} protein. Measured k_p values invariably fall below 0.76, especially where generated by the technique of comparative slaughter. Some of the discrepancy in predicted and measured k_p values may have arisen from the difficulty of measuring k_p during growth, when the energy deposited as protein is small relative to that lost as heat or deposited as lipid; even the fastest-growing animals are unlikely to retain above 0.08 of ME intake as protein (Webster, 1980). Furthermore, the partitioning of energy between protein and lipid changes continually during growth (Pullar and Webster, 1977). Small errors in estimation of ME_M can result in large adjustments to estimated k_p (Thorbek, 1970; McCracken and Weatherup, 1973). Trials where ME_M is underestimated will produce higher values for k_p, k_l being relatively inflexible.

Slaughter studies have demonstrated the age dependence of k_p estimates: younger pigs have higher k_p values than older pigs, hence, the energy costs of protein deposition increase with age (Kotarbińska, 1969; Houseman and McDonald, 1973; Müller and Kirchgessner , 1974; Close, 1978). Kielanowski (1976) suggests that lower energy cost of protein deposition at younger ages is attributable to the lower proportion of amino-acid nitrogen in total nitrogen (0.78 at 10 kg live weight, 0.89 at 100 kg, Buraczewski and Pastuszewska, 1974, unpublished data), that is, for the same nitrogen retained, younger pigs comprise less true protein. This calls into question the calculation of crude protein from the nitrogen content of meat samples by N x 6.25, when for younger animals this may not be the correct multiplier. Reeds, Cadenhead, Fuller, Lobley and McDonald (1980) ascribed the decline in k_p at heavier weights to a reduction in the fraction of synthesised protein that is deposited.

As a general rule, efficiencies of energy utilisation for protein deposition produced by slaughter experiments range from 0.49 in milk-fed piglets (Kielanowski and Kotarbińska, 1970) to 0.35 in older animals (30-90 kg, Kotarbińska, 1969); a k_p value of 0.43 would be compatible with the suggestion that energy costs of protein deposition are identical to those of lipid deposition at 54 MJ ME kg^{-1} deposited (Pullar and Webster, 1977). There is little evidence of differences in k_p and k_l between breeds of pig; discrepancy in k_p between boars and castrates just failed to reach significance due to high standard errors associated with the coefficients (Walach-Janiak *et al*, 1980).

From Table 1.8 it is apparent that the value obtained with the 36 pigs on trial is the lowest estimate of k_p, but the fact that no other experiments have used animals weighing more than 110 kg live weight

lends support to the proposition that energy costs of protein deposition increase with live weight, reducing the efficiency with which energy is utilised for protein growth. Comparison of the k_p value of 0.27 with those of 0.32 (Walach-Janiak *et al*, 1980) and 0.35 (Kotarbińska, 1969) can be construed that between 100 and 200 kg live weight the increase in energy cost of protein deposition is less pronounced than in the range 20 to 100 kg live weight; conversely, the increase in energy cost of protein deposition may proceed at a constant rate per kg increment in live weight, but that in this instance the additional energy costs are included in the maintenance estimate rather than being exclusively associated with protein deposition. Thus the true physiological meaning to energy cost of protein deposition and efficiency of energy utilisation for protein deposition is awkward to define, particularly as the energy cost of milk protein is very much lower than that of empty body protein so that the higher cost of the latter cannot be wholly ascribed to protein synthesis (Kielanowski, 1976). Moe, Tyrrell and Flatt (1970) found the maintenance requirement of lactating cows to be 0.18-0.28 higher than in dry cows, suggesting the former to be subject to an elevation in metabolic rate. By analogy, it could be assumed that in growing animals synthesis of body protein is associated with an accelerated rate of metabolism, and that this would be reflected in the energy cost of protein deposition and k_p estimates.

SUMMARY

Boars, gilts and castrates fed to appetite from weaning onwards appeared to reach a plateau in daily protein and lean gains by, or shortly after, 20 kg live weight and 55 days of age. This achievement was attributable to their high voluntary feed intakes for age; early on in the growth phase, castrated male pigs had the highest daily intakes and

the greatest daily protein and lean gains. Intake advantage was later superceded by potential for protein growth, and entire males established their supremacy over the other two sexes of pig. The margin in daily protein gain, 20-150 kg live weight, between the 'best' boar and 'worst' castrate amounted to 74 g protein daily. Maximum achieved daily protein gains were 0.162, 0.123 and 0.135 kg for a boar, gilt and castrate respectively, in association with daily lean gains of 0.324, 0.275 and 0.305; these deposition rates were obtained with pigs from one litter and are average values for the live-weight range 20 to 150 kg. Boars reached the highest plateaux for daily protein accretion and experienced the most gradual decline in deposition rate at heavier live weights, this being consistent with their greater protein growth potential and later-maturing characteristics.

Backfat depth at the P2 position was a useful predictor of carcass lean content, but a closer correlation was obtained when weight of dissected carcass lean was related to backfat depth at P2 together with a scaling factor for pig live weight.

Having ascribed certain limits to daily protein and lean deposition rates, there remains the situation of young pigs being prevented from attaining potential protein growth by voluntary or imposed intake restraint. The next Section will examine the consequences for protein and lean gains of removal from the sow. Moreover, the plasticity of protein deposition rate, particularly any intrinsic ability to recoup protein gain forgone during a growth check is assessed in young pigs by a restriction-refeeding serial slaughter trial. While wishing for continuous, uninterrupted growth from birth to slaughter, most pig producers would admit that checks in growth occur at weaning; this being so, it is of concern whether or not weaned pigs possess an ability to ameliorate the effects of growth setbacks. To a considerable extent, post-weaning recovery will be dictated by the properties of the diet offered; attention will be directed towards the influence of diet quality on feed intake and composition of the daily liveweight gain in the young pig post-weaning.

SECTION II

Growth, Body Composition and Feed Intake of Young Pigs Around Weaning

INTRODUCTION

Earlier work on body composition in 'normal' young pigs provides a standard against which composition changes can be assessed. Wood and Groves (1965) noted a reduction in body water content of suckled pigs from 0.83 at birth to 0.67 at 15 days of age, but the material on which these determinations were made was inclusive of gut contents. Manners and McCrea (1963) chemically analysed the whole empty bodies of 15 suckled pigs between the ages of 0 and 28 days, in support of which, Elsley (1964) provided empty body compositions of 233 suckled pigs at 0, 21 and 56 days of age. Details of the empty body compositions were:

	Days of age							
	0[1]	0[2]	2[1]	7[1]	14[1]	21[2]	28[1]	56[2]
No. of pigs	3	88	3	3	3	55	3	90
Live weight (g)	1520		1815	3221	5563		9928	
Empty body-weight (g)	1450	1003	1741	3044	5284	5340	9651	16220
Proportions in the empty body								
Lipid	0.012	0.014	0.023	0.101	0.151	0.142	0.183	0.146
Protein (N x 6.25)	0.120	0.110	0.136	0.144	0.146	0.144	0.148	0.146
Water	0.836[3]	0.815	0.803	0.725	0.673	0.686	0.636	0.678
Ash	0.042	0.035	0.038	0.031	0.030	0.028	0.036	0.031

[1]Manners and McCrea (1963)

[2]Elsley (1964)

[3]Dry matter was determined indirectly by difference, therefore the estimate of water content at birth will be less accurate due to inclusion of carbohydrate (glycogen can comprise 0.10-0.13 of the dry matter at birth).

Elsley (1964) also observed age-based changes in the composition of the fat-free body mass; water content decreased with advancing age,

so increasing the proportions of protein and ash. A further striking feature of early growth was the great similarity in deposition rate for protein and lipid (between 21 and 56 days of age), suggesting that a certain amount of lipid deposition was an integral part of pig development.

A picture emerged of a general reduction in water content of suckled pigs between birth and 56 days of age, or alternatively, the protein content of lean and lipid content of adipose tissue were augmented over time (Spray and Widdowson, 1950; Lucas, 1968). The most profound drop in water content, and rise in lipid content, occurred during the first week of independent life. Between 7 and 56 days of age, protein and ash fractions of the empty body remained more or less constant at around 0.15 and 0.031 respectively.

A. GROWTH OF BODY TISSUES IN YOUNG WEANED PIGS

[see Appendix 2.1]

A fall in liveweight gain to zero after weaning cannot be regarded as indicative of static body composition in the young weaner. Data from earlier experiments were used by Whittemore, Aumaitre and Williams (1978) to examine changes in body composition post-weaning. These studies form the natural precursor to the experimental series (concerned with protein growth in young pigs) central to this Section and are therefore described in some detail.

In the course of four trials carried out at Edinburgh between 1972 and 1976, 133 baby pigs were slaughtered and the chemical compositions of their empty bodies determined. The original objectives of the trials were as follows:

1. Comparison of growth potential, Hampshire vs Saddleback pigs (Whittemore and Illius, 1974).
2. Comparison of the nutritional value for weaners of cooked potato flake and maize meal (Whittemore, Taylor and Crooks, 1974).
3. Comparison of the nutritional value for weaners of dried microbial cells and white fish meal at high inclusion rate.
4. Dried microbial cells vs white fish meal at low inclusion rate (Whittemore, Moffat and Taylor, 1976).

A summary of experimental details is given in Table 2.1.

For the duration of each experiment, pigs were kept in individual pens fitted with nipple drinkers and troughs designed to minimise spillage. Chemical compositions of pigs slaughtered at the start of each experiment were used to predict the initial compositions of remaining pigs. Linear regression analysis was used to describe the relationship between weights of body tissues and weight of the empty body, the composition of the liveweight gain, and intakes of digestible energy (DE) and digestible crude protein (DCP).

Effect of weaning on the composition of the empty body and of the liveweight gain

In all four experiments, no appreciable liveweight gain was made for up to a week after weaning (Figure 2.1). Where daily feed intakes were recorded from the time of weaning (Experiments 1 and 2), amounts of feed consumed were small at between 50 and 200 g day^{-1}.

Pigs slaughtered "off the sow" had similar percentage body compositions, irrespective of age or breed, and in concurrence with the findings of Elsley (1964) for large numbers of suckled pigs. The combination of removal from the sow at 14 days of age and delay of

TABLE 2.1: Summary of experimental details

Experiment	Diet	No. of pigs	Breed	Age at weaning (days)	Age at slaughter (days)	Diet composition: MJDE kg^{-1} DM	gDCP kg^{-1} DM	DE:DCP
1	-	8	Hampshire	28	28	Suckled by sow and offered creep		
	-	8	Saddleback	28	28	Suckled by sow and offered creep		
	DSM[1]	9	Hampshire	28	55	19.9	297	0.067
	DSM	9	Saddleback	28	55	19.9	297	0.067
2	-	13	Large White x Landrace	21	21	Suckled by sow and offered creep		
	CPF[2]	9	Large White x Landrace	21	53	16.2	168	0.096
	M[3]	9	Large White x Landrace	21	53	15.3	174	0.088
3	-	19	Large White x Landrace	14	21	15.5	217	0.071
	DMC[4]	15	Large White x Landrace	14	42	15.6	219	0.071
	WFM[5]	15	Large White x Landrace	14	42	15.4	214	0.071
4	DMC[6]	9	Large White x Landrace	14	42	15.8	176	0.090
	WFM[7]	10	Large White x Landrace	14	42	15.6	162	0.096

[1] 0.5 dried skim milk, 0.1 dried whole milk, 0.13 herring meal and oat flakes, 0.05 fat, 0.05 sucrose, 0.03 glucose
[2] 0.78 dried potato flake, 0.1 soya bean meal, 0.1 white fish meal
[3] 0.78 maize meal, 0.1 soya bean meal, 0.1 white fish meal
[4] 0.2 dried microbial cells, 0.2 whey, 0.3 maize, 0.1 wheat, 0.175 barley
[5] 0.2 white fish meal, 0.2 whey, 0.3 maize, 0.1 wheat, 0.175 barley
[6] 0.1 dried microbial cells, 0.2 whey, 0.3 maize, 0.2 wheat, 0.175 barley
[7] 0.1 white fish meal, 0.2 whey, 0.3 maize, 0.2 wheat, 0.175 barley

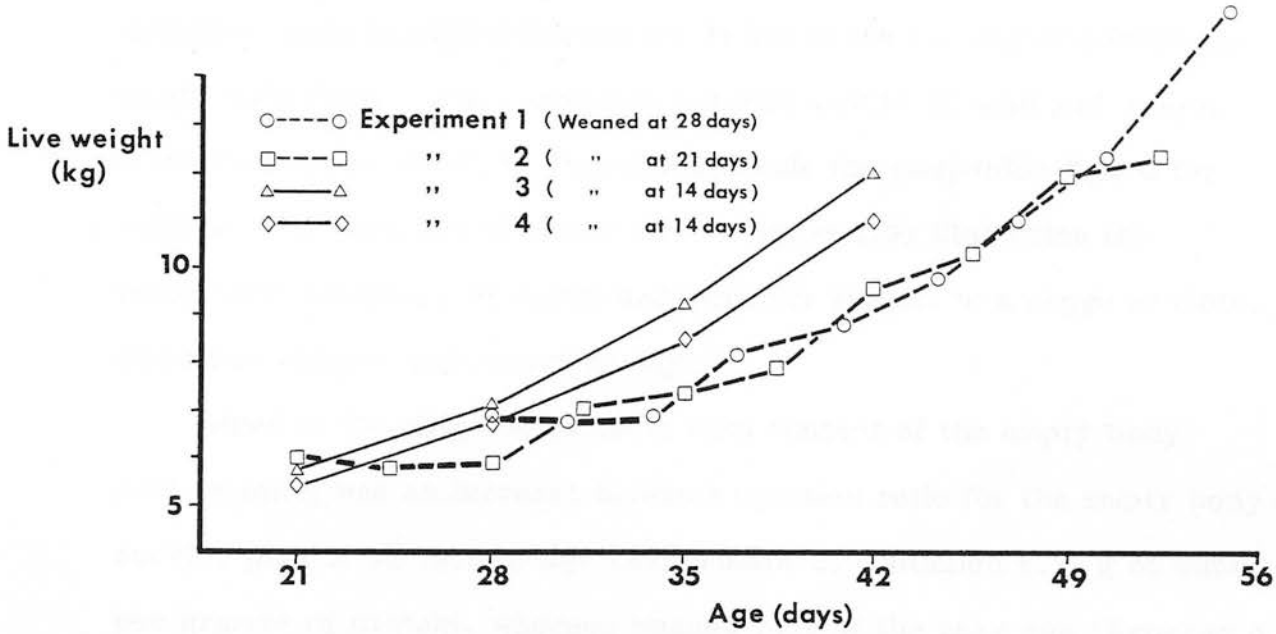


FIGURE 2.1: Pattern of liveweight gain (kg) in young weaned pigs given different dietary treatments.

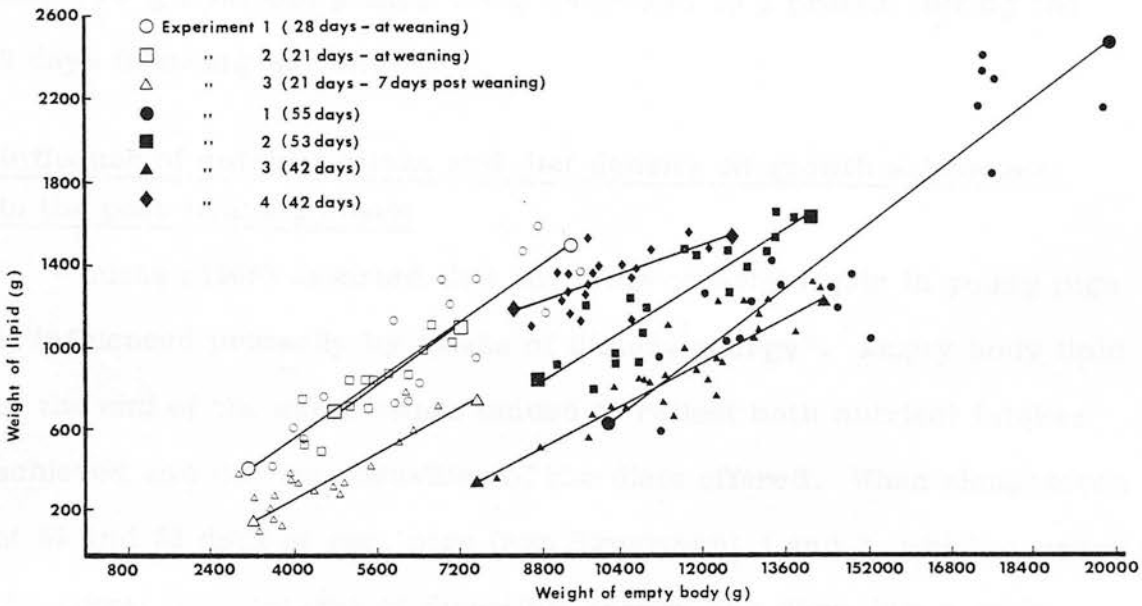


FIGURE 2.2: Lipid content of the empty body (g) in young pigs given different dietary treatments.

All diagrams in Section 2A are taken from Whittemore, Aumaitre and Williams(1978)

slaughter until 21 days (Experiment 3) led to the halving of percentage empty body lipid. The connection between weight of lipid and weight of empty body is shown in Figure 2.2, while the companion figure for weights of protein and of empty body (Figure 2.3) illustrates the remarkable constancy of empty body protein subject to a range of diets, slaughter weights and slaughter ages.

Allied to the large decrease in lipid content of the empty body post-weaning was an increase in water : protein ratio for the empty body : suckled pigs at 21 days of age (Experiment 2) contained 4.75 g of water per gramme of protein, whereas weaned pigs of the same age (Experiment 3) contained 4.93 g of water for each gramme of protein. Assuming a constant proportion of body tissues in suckled pigs, it was calculated that pigs on Experiment 3 (weaned at 14 days, slaughtered at 21 days) lost 324 g lipid and gained 254 g water and 25 g protein during the 7 days following weaning.

Influence of nutrient intake and diet density on growth subsequent to the post-weaning check

Lucas (1968) asserted that the "rate of weight gain in young pigs is influenced primarily by intake of dietary energy". Empty body lipid at the end of the experiments tended to reflect both nutrient intakes achieved and nutrient densities of the diets offered. When slaughtered at 55 and 53 days of age, pigs from Experiment 1 and 2, which consumed the lowest daily intakes of digestible energy and digestible protein (0.63 and 0.61 MJ DE kg EBW^{-1} day^{-1} respectively; 9.4 and 6.6 g DCP kg EBW^{-1} day^{-1}), contained lower percentages of lipid in the empty body than at the start of the experiments. Pigs on Experiment 3 slaughtered at 42 days (having consumed 0.99 MJ DE and 13.9 g DCP kg EBW^{-1} day^{-1}) had returned to virtually identical lipid content with

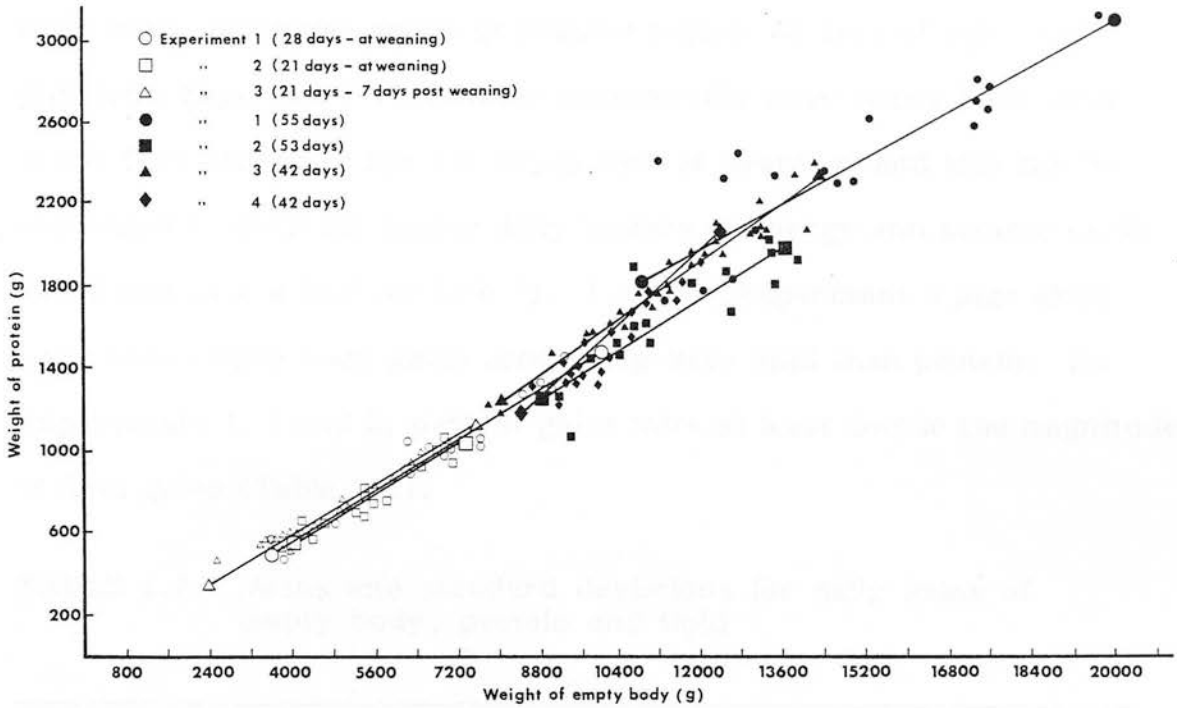


FIGURE 2.3: Protein content of the empty body (g) in young pigs given different dietary treatments.

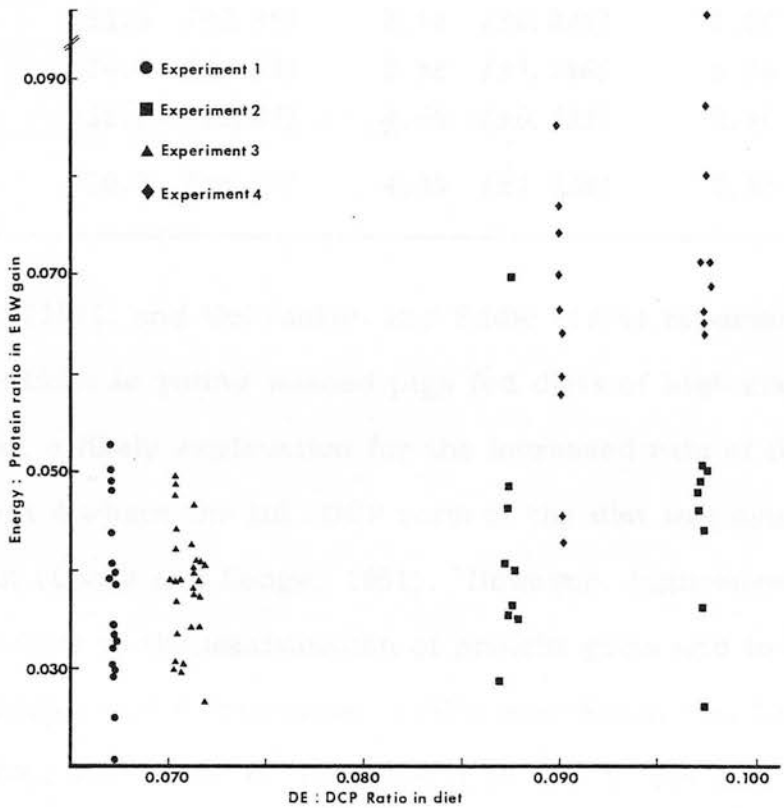


FIGURE 2.4: Relationship between energy : protein ratio in the empty body gain and dietary energy : protein ratio.

their initial slaughter group of suckled pigs at 21 days of age. Only pigs from Experiment 4 contained considerably more empty body lipid at the final slaughter age (42 days) than at weaning, and this can be attributed to their far higher daily intakes of energy and protein (1.33 MJ DE and 14.3 g DCP kg EBW^{-1}). Further, Experiment 4 pigs alone made daily empty body gains comprising more lipid than protein; for Experiments 1, 2 and 3, protein gains were at least double the magnitude of lipid gains (Table 2.2).

TABLE 2.2: Means and standard deviations for daily gains of empty body, protein and lipid

Experiment	Empty body (g)	Protein (g kg EBW^{-1})	Lipid (g kg EBW^{-1})
1	29.0 *(±2.14)*	5.09 *(±0.759)*	1.72 *(±1.013)*
2	21.3 *(±2.96)*	3.14 *(±0.475)*	1.50 *(±0.818)*
3	34.7 *(±5.83)*	5.88 *(±1.186)*	2.36 *(±1.030)*
4	32.7 *(±3.81)*	4.95 *(±0.635)*	5.98 *(±1.086)*
All	30.2 *(±6.57)*	4.93 *(±1.320)*	2.85 *(±1.981)*

Jordan (1974) and McCracken and Eddie (1974) reported enhanced energy retentions in young weaned pigs fed diets of high energy : protein ratio, a likely explanation for the increased rate of lipid gain in Experiment 4 where the DE : DCP ratio of the diet was closest to that in sows' milk (Lucas and Lodge, 1961). However, high-energy diets may not be conducive to the maximisation of protein gains and to achieve the latter goal Müller and Kirchgessner (1974) and Wilson and Leibholz (1979) suggested DE : DCP ratios in the range 0.06 to 0.07 for pigs between 3 and 42 days of age. Slightly older pigs (21-55 days) in Experiments 1 and 3 fed diets with DE : DCP ratios of 0.067 and 0.071 realised the highest daily protein gains.

Energy : protein in the gain showed great variation for a particular dietary DE : DCP, and the relationship between these two parameters was further confounded by differences in feed intake between experiments (Figure 2.4). Nevertheless, there was good agreement between daily energy intakes (MJ DE kg EBW^{-1}) and daily energy retentions (MJ kg EBW^{-1}):

$$\text{DE intake} = \underset{(\pm 0.193)}{2.99}\ \text{Energy retained} + \underset{(\pm 0.0464)}{0.238} \qquad r = 0.86$$

which suggests that DE intake was converted to energy in the empty body with an efficiency of 0.33, a much lower value than others in the literature, for example, 0.70 (Close, Verstegen and Mount, 1973), but one which may be consistent with a period of measurement of tissue gains which includes a phase of lipid catabolism. The previous equation also indicated that at zero energy retention the daily intake of DE was 0.238 MJ kg EBW^{-1} (or 0.375 MJ $kg^{0.75}$ EBW^{-1}) at an average body weight of 8.7 kg.

In conclusion, weight stasis following weaning can be ascribed to a depression in nutrient intake and can be said to mask a loss of lipid from the empty body. The proportion of the empty body as protein remains more or less unchanged. On recovery from this post-weaning growth check subsequent gains of lipid, and to a lesser extent protein, will be influenced by nutrient intake and the DE : DCP ratio in the diet. In particular, a weaner diet of high nutrient density will promote rapid lipid gains and so ensure that the return to pre-weaning body tissue proportions is achieved with greater alacrity.

B. CHANGES IN DISSECTED AND CHEMICAL COMPONENTS OF PIGS AFTER WEANING

[see Appendix 2.2]

The trials described in Part A established that as a sequel to weaning, young pigs ate very little solid food and catabolised body lipid to resolve their temporary energy deficit. While most pertinent to the study of body composition changes in young pigs, these trials had not been specifically designed for such a purpose and, amongst others, the following questions still remained unanswered:

At what rate is lipid depleted from body lipid stores?

Where, anatomically, does lipid loss occur?

If lipid is eroded from the empty body, is extra water retained over and above that usually associated with protein during positive growth?

If there is an influx of water to counterbalance lipid loss, does water enter "shrinking" adipose cells?

A serial slaughter experiment was undertaken in which conventional procedures for carcass evaulation were refined somewhat with the aim of arriving at a more subtle interpretation of body composition changes following weaning. Carcasses were physically separated into anatomical fractions and these dissected fractions were homogenised for chemical analysis, as opposed to the previous practice of homogenising the whole empty body.

Thirty-two Large White x Landrace pigs from eight litters were allocated at 21 days of age and 6.1 (±0.14) kg live weight to one of 16 treatments (1 pair of pigs per treatment) involving:

(i) 4 levels of feeding - suckled by the sow

- 200
- 100
- 50

g early-weaning diet day^{-1}

The feed allowances for weaned pigs were within the range of feed intakes achieved voluntarily by pigs during the week following weaning on Part A trials. 200 g diet day^{-1} represented the approximate daily requirement for maintenance by pigs of six kg live weight.

(ii) 4 ages at slaughter - 2, 4, 6 and 8 days after allocation to dietary treatment.

The early-weaning diet contained 190 g DCP and 14.2 MJ DE kg^{-1} fresh weight (Tullis and Whittemore, 1980); details of its ingredient and chemical composition are given in Table 1.1, Section I. Early-weaning diet was also offered as a creep feed to pigs remaining with the sow.

Pigs were slaughtered by administration of a lethal dose of sodium pentabarbitone. Immediately prior to slaughter, 10 ml samples of blood were taken from the aorta for free fatty acid determinations according to the method of Wood, Gregory, Hall and Lister (1977). Dead pigs were weighed and bled, the stomach and intestines were removed and their contents discarded. The non-carcass (NC) fraction was then assembled from: empty alimentary tract, pluck, blood, internal organs, kidneys and flare fat, head, feet, tail. A second fraction, carcass fatty tissue (CFT) comprised the skin, subcutaneous fat and cutaneous truncii. Carcass muscle plus bone, together with intermuscular fat, made up the third fraction (CMB). The three fractions were weighed and minced individually through a 1.5 mm screen. Chemical analysis was for gross energy (GE), nitrogen and ash, while lipid was calculated

from the equation: Lipid = (GE - 0.1475 N) / 0.0393 (Whittemore *et al*, 1976).

The empty body weights, dissected fraction weights and chemical compositions of pigs at day 0 of the experiment were predicted from linear regression of these characters on live weight at slaughter for suckled pigs. Two weaned pigs were excluded from the statistical analysis due to incomplete dissection data (offered 200 g day^{-1}, slaughtered at 4 and 8 days after allocation to treatment). Within the same feed level treatment two pigs failed to consume the total feed allowance (200 g day^{-1} slaughtered after 2 days: consumed 49 and 80 g day^{-1}, indicated by the letter 'R' in Figures 2.5 to 2.9).

Effect of weaning on rate of gain in empty body and dissected fractions

There are attendant difficulties in calculating daily gains of empty body and body components by pigs after weaning, particularly where gains are negative and pig numbers are small. To overcome these problems, the gains presented for this trial will be cumulative gains, that is, the total increment achieved between estimated initial composition at day 0 and measured composition at slaughter. Rates of gain for suckled pigs have been derived by linear regression of cumulative gains on days after allocation to treatment.

Cumulative empty bodyweight gains (CEBG) of suckled pigs increased steadily after allocation to treatment:

$$\text{CEBG (g)} = \underset{(\pm 12.97)}{354.1} \text{ days after allocation} - \underset{(\pm 71.02)}{280.7} \qquad r = 1.00$$

Reference to Figure 2.5 indicates that cumulative empty body gains by weaned pigs did not reflect the duration of feed level treatment (2, 4, 6 or 8 days). However, the magnitude of these gains was conditioned

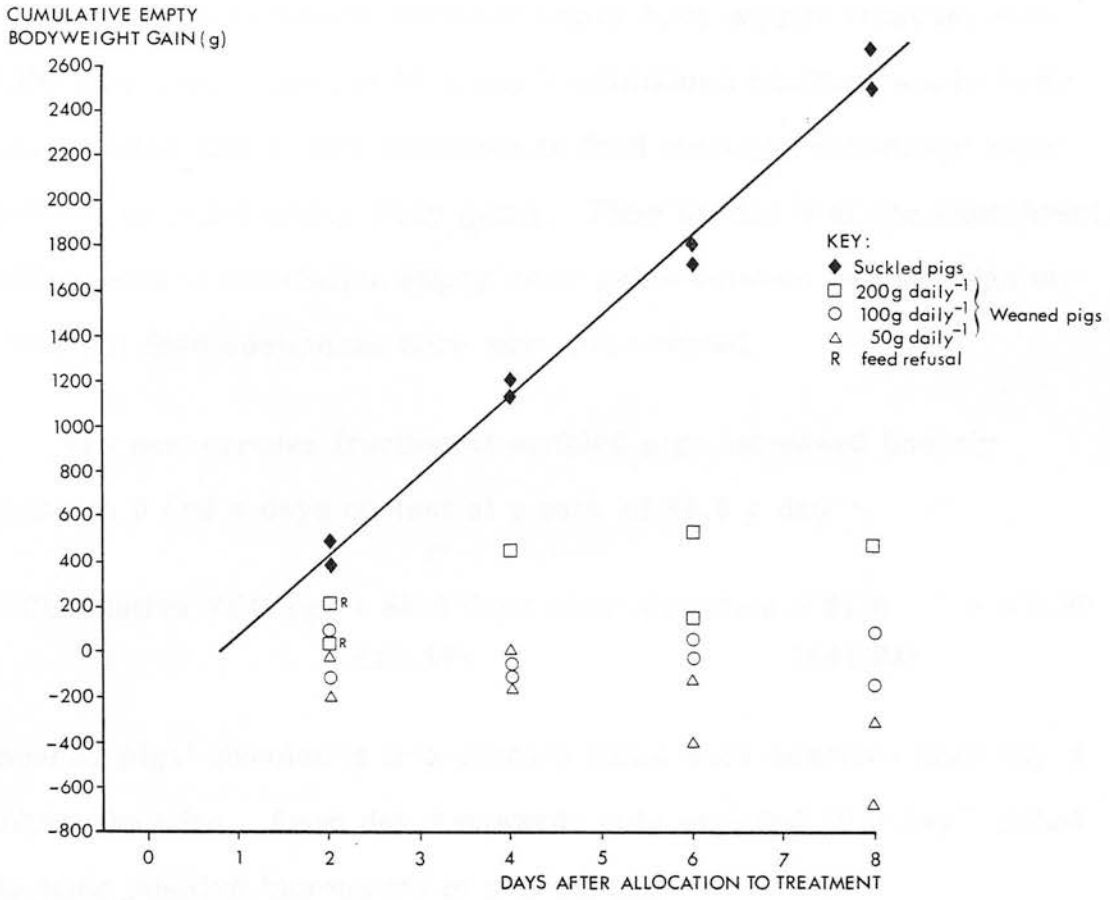


FIGURE 2.5: Cumulative empty bodyweight gains (g) between 21 and 29 days of age by suckled pigs (♦) and weaned pigs offered 200 (□), 100 (○) and 50 (△) g early-weaning diet per day.

'R' denotes feed refusals.

by feed intake: pigs offered 200 g day^{-1} made positive cumulative empty body gains throughout their time on test, pigs given 100 g day^{-1} remained more or less at constant empty body weight (that is, zero CEB gain), and pigs fed 50 g day^{-1} maintained constant empty body weight until day 4 after allocation to feed level but thereafter experienced negative empty body gains. Thus by day 8 of the experiment, differences in cumulative empty body gains between weaned pigs on different feed allowances were more pronounced.

The non-carcass fraction of suckled pigs increased linearly between 0 and 8 days on test at a rate of 88.6 g day^{-1}:

$$\underset{\text{Cumulative NCG (g)}}{} = \underset{(\pm 7.47)}{88.6} \times \underset{\text{days after allocation}}{} - \underset{(\pm 40.93)}{91.0} \qquad r = 0.98$$

Weaned pigs' cumulative non-carcass gains were negative until day 4 after allocation. From day 4 onwards only pigs fed 50 g day^{-1} failed to make positive increments in non-carcass.

Carcass fatty tissue was the dissected fraction most affected by losses following weaning. Pigs on the lower feed allowances (50 and 100 g day^{-1}) endured the greatest losses in CFT, although carcass fatty tissue gains were negative for weaned pigs at each feed level and slaughter age. The rate of carcass fatty tissue depletion approximated to 22 g day^{-1} for all weaned pigs together. Conversely, suckled pigs gained 65 g carcass fatty tissue daily:

$$\underset{\text{Cumulative CFTG (g)}}{} = \underset{(\pm 9.36)}{65.4} \times \underset{\text{days after allocation}}{} - \underset{(\pm 51.30)}{29.2} \qquad r = 0.93$$

Mean carcass muscle plus bone gains by weaned pigs were zero for the duration of the trial: pigs offered 200 g day^{-1} always made

positive CMB gains, pigs fed 50 g day^{-1} invariably made negative CMB gains, and pigs fed 100 g day^{-1} were intermediate between the other two feed levels. Suckled pigs gained 164 g carcass muscle plus bone daily:

Cumulative CMBG (g) = 164.3 days after allocation - 94.9 r = 0.93
(±23.36) (±127.97)

From the relationship between dissected fraction gains by suckled pigs and days after allocation to treatment it can be estimated that cumulative gains in non-carcass, carcass fatty tissue and carcass muscle plus bone did not rise above zero until after 1.03, 0.45 and 0.58 days on test respectively. This implies that even pigs remaining with the sow were subject to some disturbance (for example, removal of other pigs from the litter) and as a result went for up to a day without growth of the dissected body fractions.

Influence of weaning on the rate of gain in chemical components of the empty body

Suckled pigs gained 202 g water, 69 g lipid and 57 g protein daily between day 0 and day 8. Lipid gains (LG) proved rather more variable than either water (WG) or protein gains (PG):

Cumulative WG (g) = 202.0 days after allocation - 98.6 r = 0.99
(±13.12) (±71.87)

Cumulative LG (g) = 68.9 days after allocation - 78.4 r = 0.89
(±14.27) (±78.15)

Cumulative PG (g) = 57.3 days after allocation - 51.2 r = 0.93
(±8.49) (±46.49)

The two weaned pigs fed 50 g day^{-1} for 8 days were in negative balance for water and protein gains by day 8 of the trial. All other weaned pigs made positive cumulative water and protein increments.

Lipid gains (Figure 2.6) were negative for weaned pigs at each feed level and slaughter age. Between days 0 to 6 on test, lipid losses averaged 36 g day^{-1}; from day 6 onwards, the rate of lipid depletion abated somewhat. This pattern of lipid catabolism was corroborated by plasma free fatty acid concentrations; the latter were highest at day 2 after allocation to feed level, that is, day 2 after weaning (range 800-1500 µmol. $litre^{-1}$) and declined to 300-600 µmol. $litre^{-1}$ by day 8. Plasma free fatty acid concentration also showed clear differentiation according to feed allowance, with by far the greatest mobilisation of lipid being elicited by feeding 50 g day^{-1} after weaning:

200 g day^{-1}	FFA (µmol $litre^{-1}$)	=	85 (±9) days after allocation	+ 1056 (±51)
100 g day^{-1}	FFA	=	82 (±17) days after allocation	+ 1075 (±92)
50 g day^{-1}	FFA	=	221 (±58) days after allocation	+ 2227 (±318)

Dissected fraction and chemical component composition of the empty body gain

Cumulative non-carcass gains represented 0.23 of cumulative empty body gains; this applied to both positive and negative empty body gains and was irrespective of dietary treatment:

All pigs Cumulative NCG (g) = 0.23 (±0.013) CEBG (g) + 29.9 (±11.79) r =0.95

Therefore, pigs had to lose more than -132 g empty body weight before non-carcass gains became negative.

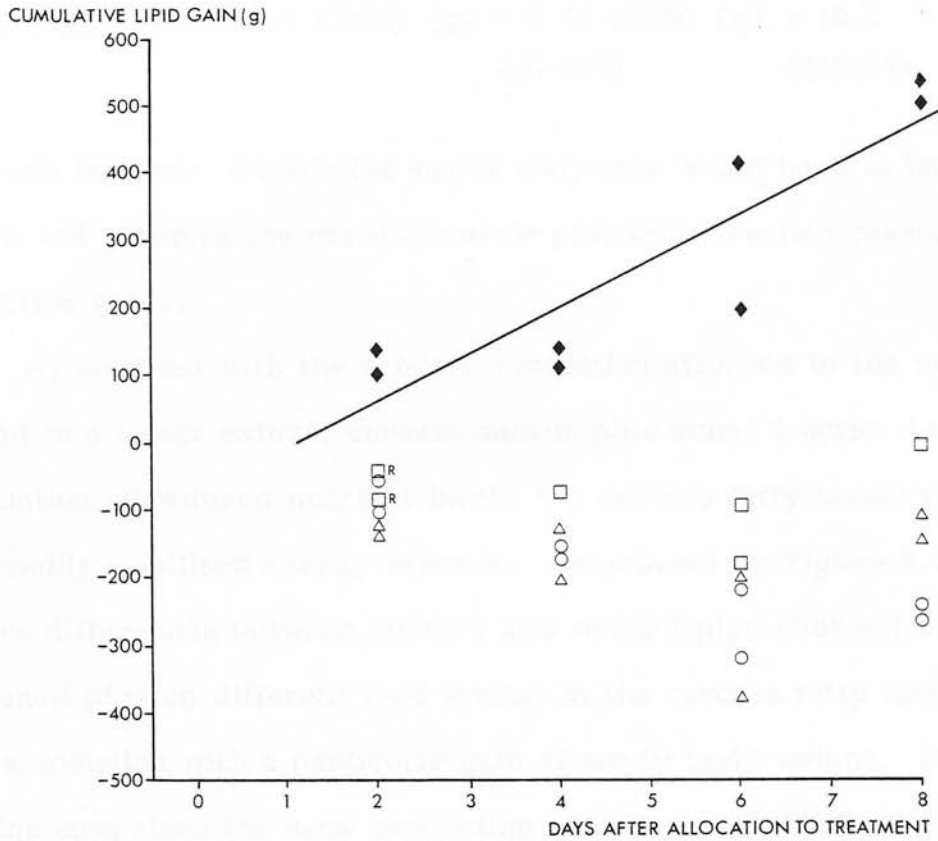


FIGURE 2.6: Cumulative lipid gains (g) between 21 and 29 days of age by suckled pigs (♦) and weaned pigs offered 200 (□), 100 (○) and 50 (△) g early-weaning diet per day.

Similarly, there were no significant differences between suckled and weaned pigs in the proportion of carcass muscle plus bone in the empty body gain:

All pigs Cumulative CMBG (g) = 0.46 CEBG (g) + 29.6 r = 0.98
(±0.019) (±17.05)

In this instance, cumulative empty body loss would have to be greater than -64 g before the carcass muscle plus bone fraction ceased to make positive gains.

By contrast with the relative protection afforded to the non-carcass (and to a lesser extent, carcass muscle plus bone) fraction in a situation of reduced nutrient intake the carcass fatty tissue provided a readily mobilised energy reserve. As evinced by Figure 2.7, there were differences between suckled and weaned pigs (but not between weaned pigs on different feed levels) in the carcass fatty tissue gained in association with a particular gain of empty body weight. Empty body gains comprised the same proportion of CFT for suckled and weaned pigs, as indicated by their common slope ($b = 0.190 \pm 0.0144$, $r = 0.84$) but intercepts were significantly disparate (±14.96 for suckled pigs and -111.90 for weaned pigs, $P < 0.01$). By extrapolation, suckled pigs needed to deposit more than -79 g empty body weight before CFT gains became positive whereas weaned pigs required empty body gains in excess of 590 g to accomplish the same state. Bearing in mind the observed variation in carcass fatty tissue gains by suckled pigs, the absolute magnitude of these empty body gains should be regarded with caution.

All pigs gained 0.53 water and 0.14 protein with each unit increment of empty body:

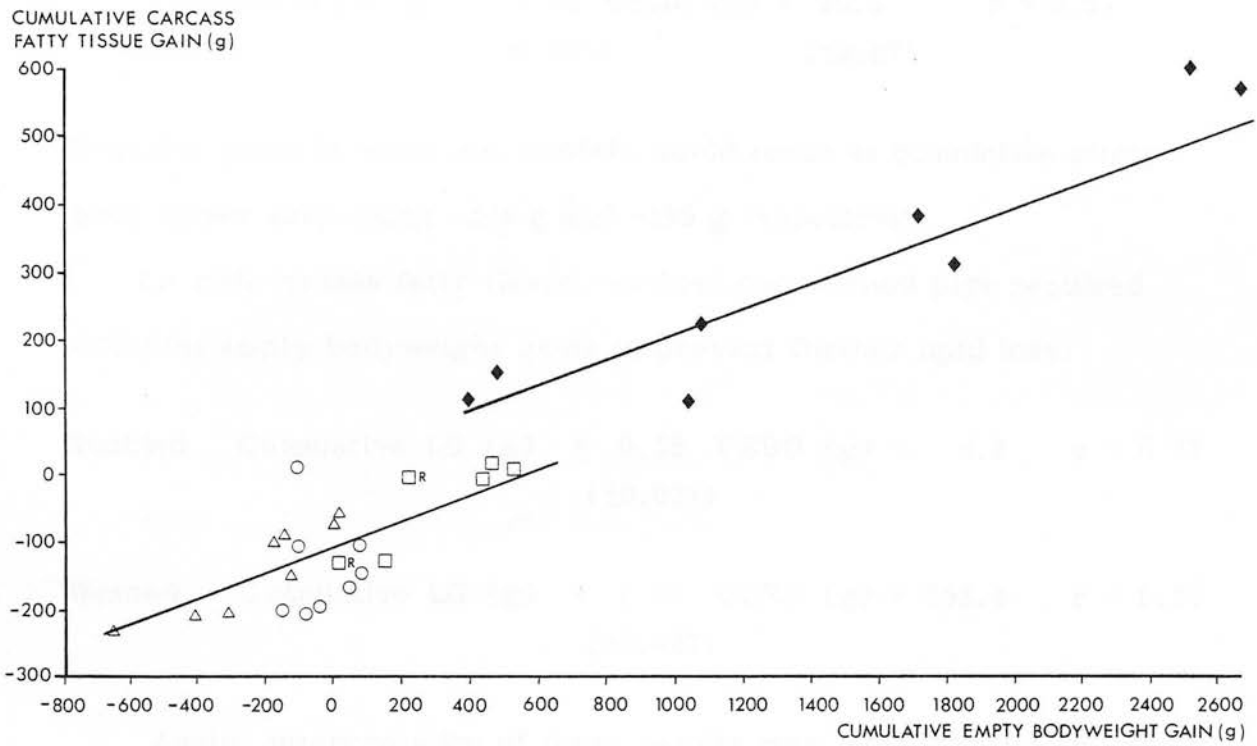


FIGURE 2.7: Cumulative carcass fatty tissue gains (g) as a function of cumulative empty bodyweight gains (g) for suckled pigs (♦) and weaned pigs offered 200 (□), 100 (○) and 50 (△) g early-weaning diet per day.

Cumulative WG (g) = 0.53 CEBG (g) + 148.3 r = 0.98
(±0.019) (±16.81)

Cumulative PG (g) = 0.14 CEBG (g) + 28.3 r = 0.95
(±0.009) (±8.07)

Negative gains in water and protein would occur at cumulative empty body losses surpassing -278 g and -199 g respectively.

As with carcass fatty tissue, suckled and weaned pigs required different empty bodyweight gains to prevent further lipid loss:

Suckled Cumulative LG (g) = 0.18 CEBG (g) - 4.2 r = 0.73
(±0.027)

Weaned Cumulative LG (g) = 0.18 CEBG (g) - 152.4 r = 0.73
(±0.027)

Again, interpretation of these results must take into account the variation in suckled pigs' lipid gains, but despite the lipid content of the empty body gain being fixed for both groups at 0.18, a mere 23 g of CEB gain secured lipid reserves for suckled pigs whereas a massive 838 g CEB gain was required by weaned pigs to do likewise.

Consequences of weaning for the carcass fatty tissue fraction

It has become apparent that the carcass fatty tissue is the principal location in the young pig's body for post-weaning composition changes: lipid is the chemical component undergoing the most rapid depletion following weaning and carcass fatty tissue represents the major lipid-containing fraction in the empty body.

The lipid content of dissected carcass fatty tissue decreased with time after weaning:

day	0	0.505	suckled pigs
	2	0.416	weaned pigs
	4	0.400	
	6	0.343	
	8	0.366	

Once again, day 6 seems to have been the 'turning-point' for weaned pigs, after which lipid losses began to be reversed. Elsley (1963a) restricted the feed intake of early-weaned pigs and found their 56-day carcasses to contain only 0.58 of the subcutaneous fat mass found in suckled contemporaries; lipid content of restricted pigs' subcutaneous fat was 0.40 as compared to 0.59 for suckled pigs. Therefore, as a result of voluntary or imposed feed intake restriction, the carcass fatty tissue of weaned pigs was reduced in mass and included less lipid than the carcass fatty tissue of suckled pigs. Loss of lipid from the CFT fraction would automatically lower the dry matter of that fraction due to a *pro rata* increase in the proportion of water.

However, the most controversial question has still to be resolved: Does extra water enter adipose tissue as a corollary to lipid catabolism?

There were no differences between suckled and weaned pigs in the dry matter contents of the non-carcass and carcass muscle plus bone, which eliminates these fractions of the empty body as locations for enhanced water retention. In Figure 2.8 the proportion of dry matter in the carcass fatty tissue is plotted against the proportion of lipid in the CFT dry matter. The carcass fatty tissue comprised 0.57 ($\pm$0.255) lipid in the dry matter for both suckled and weaned pigs but constants were significantly different (0.52 for suckled pigs and 0.084 for weaned pigs, $P < 0.001$, $r = 0.75$), inferring that for a given proportion of lipid in the CFT dry matter the CFT dry matter itself was lower in weaned pigs. It might have been anticipated that an influx of water

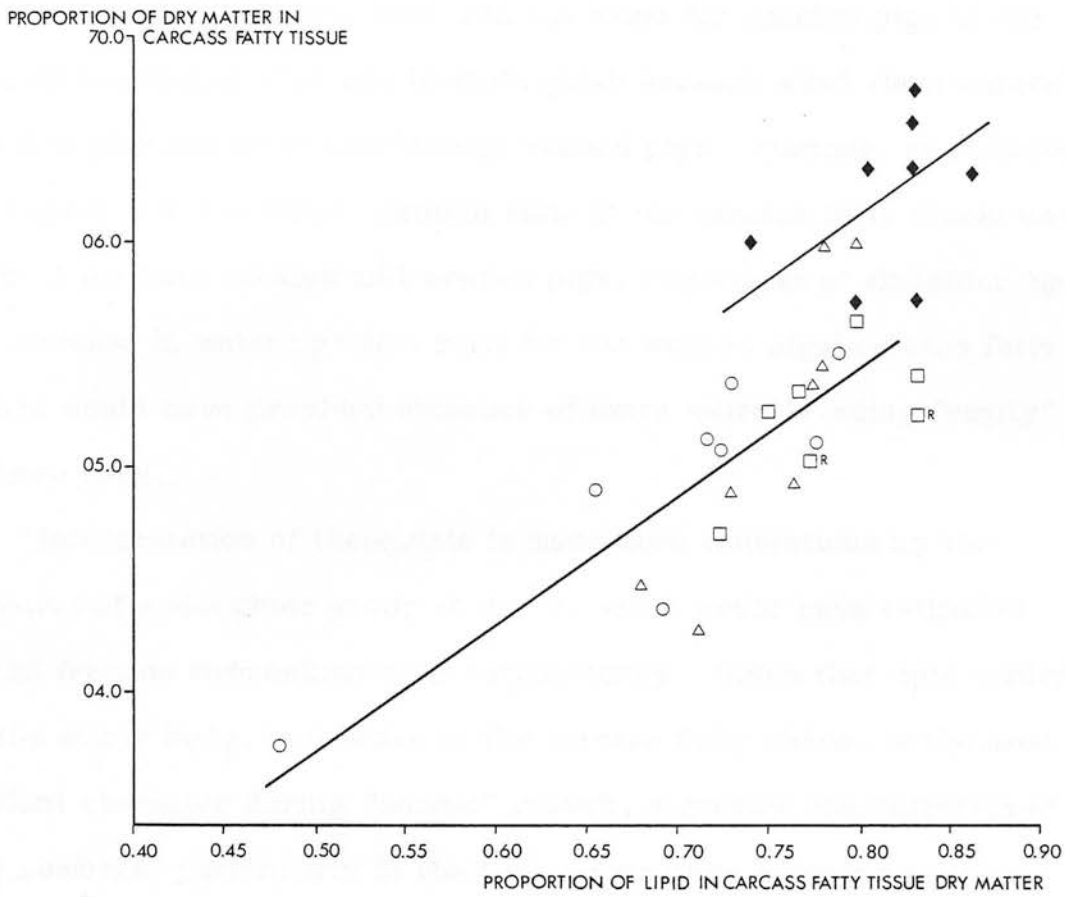


FIGURE 2.8: Proportion of dry matter in the carcass fatty tissue against the proportion of lipid in the carcass fatty tissue dry matter for suckled pigs (♦) and weaned pigs offered 200 (□), 100 (○) and 50 (△) g early-weaning diet per day.

into "shrinking" adipose tissue would produce a significantly steeper gradient to the slope for weaned pigs than the slope for suckled pigs, and one which would intercept with the slope for suckled pigs at the time of weaning to allow one to distinguish between small (less mature) suckled pigs and small (shrinking) weaned pigs. Further, as indicated by Figure 2.9, the water : protein ratio in the carcass fatty tissue was 2.98 : 1 for both suckled and weaned pigs, regardless of slaughter age. An increase in water : protein ratio for the weaned pigs' carcass fatty tissue would have provided evidence of extra water invading "empty" adipose cells.

Interpretation of these data is made more contentious by the omission of a slaughter group at day 0, which would have estimated initial fraction composition more satisfactorily. Given that lipid content of the empty body, and hence of the carcass fatty tissue, is the most deviant character during "normal" growth, a greater concentration of pig numbers, particularly in the two to four days following weaning when the most profound compositional changes took place, would have helped to discriminate between inherent variation in CFT lipid and water concentrations and differences in these parameters arising from reduced nutrient intake post-weaning.

Conclusions

Weaning at 21 days of age brought about a large reduction in empty body lipid, most of which was lost from the carcass fatty tissue (subcutaneous fat) fraction. Viewed subjectively, the young pig protected its internal organs, and to a lesser extent its skeletal muscle, by depleting its principal energy reserve to fulfil energy requirements during a transitory period of depressed appetite. Despite the relative immaturity of the pigs in this experiment, they were able to deplete

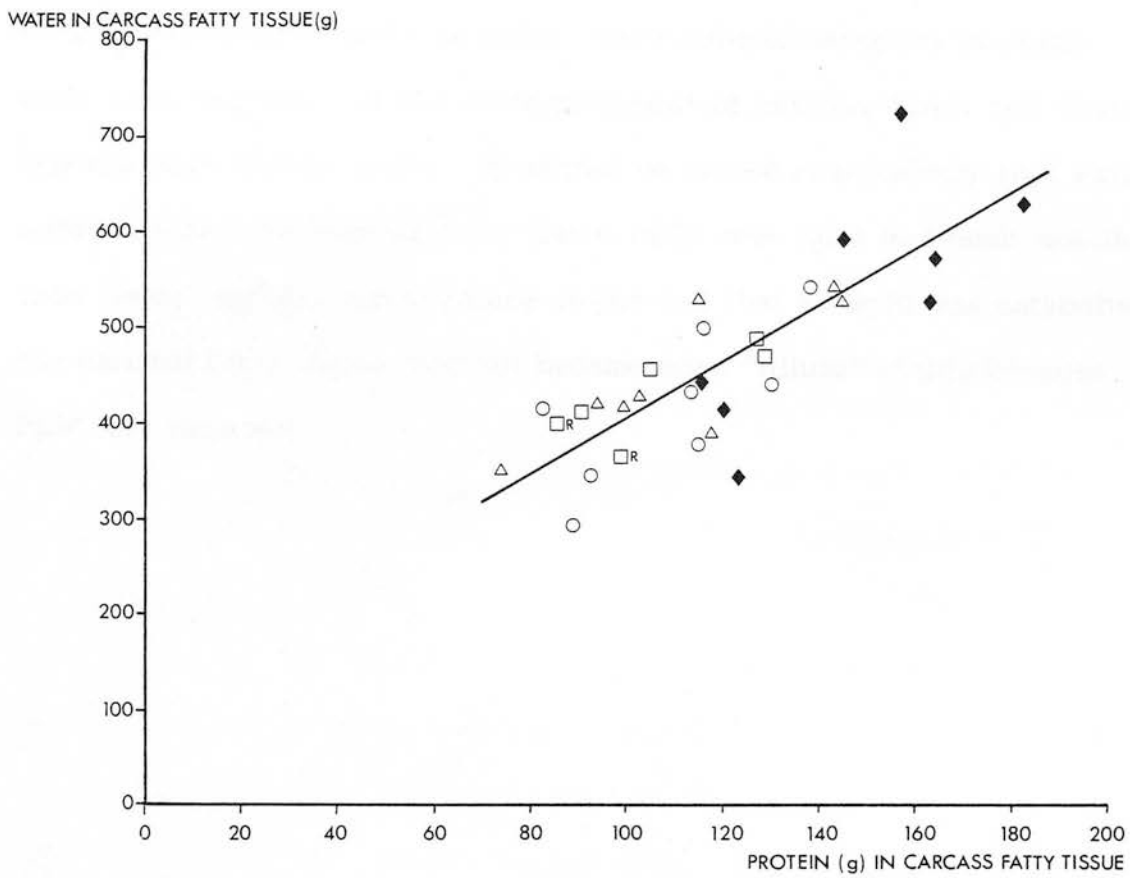


FIGURE 2.9: Weight of water in the carcass fatty tissue (g) against weight of protein in the carcass fatty tissue (g) for suckled pigs (♦) and weaned pigs fed 200 (□), 100 (○) and 50 (△) g early-weaning diet per day.

roughly 36 g lipid daily from their lipid reserves in the six days following removal from the sow. Whereas considerable post-weaning losses in empty body weight had to be experienced before gains in water and protein became negative, very substantial gains in empty body were required for the accomplishment of positive lipid, and thus carcass fatty tissue, gains. It cannot be stated conclusively that extra water entered the carcass fatty tissue cells once lipid had been mobilised from them; rather, the evidence suggested that as lipid was catabolised the carcass fatty tissue fraction became more "dilute" simply because lipid was removed.

C. CHANGES IN BODY COMPOSITION AND VOLUNTARY FEED INTAKE OF YOUNG FEMALE PIGS ACCORDING TO DEGREE AND DURATION OF POST-WEANING FEED RESTRICTION

INTRODUCTION

This experiment was designed to investigate the hypothesis that animals of high protein growth potential, young pigs post-weaning, might be able to recompense for an earlier failure to maximise protein deposition by undergoing a period of catch-up protein growth.

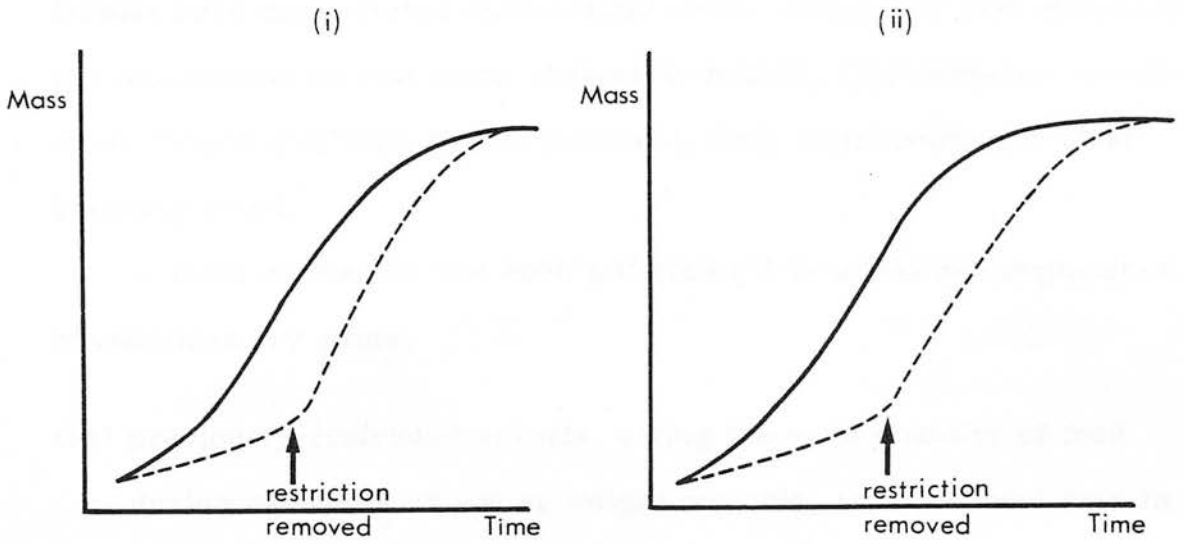
It is not the intention of this Section to provide a definitive review of literature concerned with compensatory growth. Experimental techniques for the assessment of this phenomenon have been various and the results produced equivocal, particularly in the case of compensatory protein growth.

One of the first agricultural references to the subject was by Waters (1908) who showed that undernourished beef steers could recover and reach mature weights and heights. Later Bohman (1955) defined 'compensation' as abnormally rapid growth relative to age. Two possible mechanisms for compensation were proposed by Eckles and Swett (1918):

(i) animals were able to recover from undernutrition by increasing their feed intake, and hence their rate of bodyweight gain, or

(ii) animals "caught up" with their contemporaries by prolonging the growth period, that is, continuing positive growth beyond the chronological age at which unrestricted controls cease to gain weight. Monteiro and Falconer (1966) provided an example of extended exponential growth in restricted and refed mice.

Mechanisms (i) and (ii) are represented diagrammatically overleaf. There is evidence to suggest that mechanism (i), involving enhanced



appetite once intake restriction is removed, is more relevant to circumstances of energy restriction rather than protein restriction, and in addition, that the effect is accentuated in pigs and children when high-energy diets are offered during refeeding (Ashworth, Bell, James and Waterlow, 1968; Cole, Duckworth, Holmes and Cuthbertson, 1968; Owen, Ridgman and Wyllie, 1971). In some studies compensatory feed intakes have been precluded by not allowing expression of appetite after removal of the restriction (Boaz and Elsley, 1962; Neilsen, 1964; Robinson, 1964; Fowler, 1976; Campbell and Biden, 1978; Thornton, Hood, Jones and Re, 1979), a procedure which prolongs the effects of intake restriction such that they are still apparent in the carcass at slaughter. Practical pig production would be more likely to exploit mechanism (i) than mechanism (ii) as the former would enable meat animals to recover from a period of restriction before reaching slaughter weight or age. Mechanism (ii) pertains to breeding animals, owing to the time required for complete recovery. In theory,

a complete recovery might be undesirable: if nutritionally-stunted females bred and lactated successfully (while eating less than generously-fed contemporaries and being cheaper to house), and produced normal-sized offspring of high growth potential, they would represent ideal breeding stock.

A third mechanism has been put forward as a possible explanation of compensatory gains:

(iii) previously-restricted animals, eating the same quantity of food during refeeding as age or weight controls, could convert food to gain with greater efficiency. This might be achieved if refed animals had lower maintenance requirements (Blaxter, 1962), so freeing more net energy to be utilised for growth (Brody, 1945). Alternatively, more rapid growth during refeeding might result from greater efficiency in the utilisation of energy above maintenance (Vanschoubroek, De Wilde and Van Spaendonck, 1965), possibly by depositing tissue of lower energy content (Ørskov, McDonald, Grubb and Pennie, 1976). Mechanism (iii) represents true compensation as faster gains during refeeding are achieved for no extra total feed input. If previously-restricted animals require extravagant inputs of feed during realimentation in order to recoup lost growth, then they are exhibiting catch-up gain rather than compensatory growth.

The immediate response to refeeding after a period of restriction can be measured either,

(a) by the difference in age between control and restricted and refed animals at equal body weight or component mass, or

(b) by the difference in body weight or component mass between control and restricted and refed pigs at the same age.

In the longer term there are distinct dangers associated with comparison (b) because a reduction in the difference between control and refed animals in their body weight or component mass at more advanced ages (convergence of growth curves), attributed to compensation by refed animals, could in fact be due to a slowing down in growth rate by controls. This contingency casts suspicion on claims of compensation during the late fattening period by pigs restricted in early life (for example, Duckworth, 1965).

The majority of trials studying the growth performance of realimented farm animals or human infants have commented on a marked increase in growth rate and feed conversion efficiency immediately following removal of an intake restriction (Lucas, Livingstone and McDonald, 1962; Robinson, 1964; Cole *et al*, 1968; Ashworth, 1969), with the severest intake limitations producing the greatest subsequent boost to growth rate (Wilson and Osbourn, 1960). An accelerated rate of gain, or decrease in time taken to reach slaughter weight, was reported in many of the earlier experiments on catch-up growth (Lucas *et al*, 1962; Elsley, 1963b; Vanschoubroek *et al*, 1965; Fowler, 1968; Lynch, O'Grady and Spillane, 1971; Libal and Wahlstrom, 1976; Hogberg and Zimmerman, 1978). While these findings are of interest, they cannot lay claim to demonstrate worthwhile compensatory growth because carcass evaluation was not used to pinpoint the contributions of different tissues to the faster gain. Extra gut fill, reflecting enhanced post-restriction feed intakes, would serve to reduce killing-out percentage at slaughter. A more serious depreciation of the slaughter animal's commercial value would arise if faster growth during refeeding encompassed more rapid fat deposition in the carcass. Neilson (1964) asserted that pigs restricted to 20 kg live weight under-

went compensatory growth during refeeding, but did not define the tissues constituting the regrowth, and did not permit full expression of appetite post-restriction. Panemangalore, Clark and Clark (1978) found previously-restricted rats to be capable of catching up for fat but not for protein. But it is extra protein deposition (or more cynically, extra water deposition) which is of economic importance. Kielanowski (1967) used data produced by Kotarbinska (1966) to argue that compensatory gains could incorporate enhanced protein deposition, for no extra food intake, when pigs were released from intake restriction at 60 kg live weight. Starting with pigs of the same weight (60 kg), Fowler (1976) imposed maintenance allowance for 28 days and reported that during refeeding (in which pigs were not fed to appetite) both protein and water gains were increased. Whittemore, Tullis and Hastie (1978, Section 3A) detected a heightening of nitrogen retention in 50 kg pigs following a 10-day period of nitrogen deprivation. Even very early protein restriction, of foetuses in *utero* by protein deprivation of the dams (sows: Livingston, 1962, Livingstone, MacPherson, Elsley, Lucas and Lodge, 1966; ewes: Everitt, 1968) has been found to be reversible if restricted offspring (which contained less nitrogen at birth) were fed generously *post-partum* on nutrient-dense diets.

Even where carcass studies have been undertaken, restriction and realimentation has produced conflicting results for pigs taken to commercial slaughter weight (generally 90 kg live weight). Some authors claimed an advantage in carcass leanness, consequent upon early restriction, apparent in larger eye muscle area and less carcass fat (Lucas, Calder and Smith, 1959; Elsley, 1963b; Vanschoubroek *et al*, 1965; Kotarbińska, cited by Kielanowski, 1967; Cole *et al*, 1968). Other workers did not detect any significant differences in dissected

carcasses from refed and control pigs (Frape, Hays, Speer, Jones and Catron, 1959; Lucas, Livingstone and McDonald, 1964; Duckworth, 1965), even where pigs were not fed *ad-libitum* after removal of intake restriction (Neilsen, 1964; Campbell and Biden, 1978). A further complication adds to the difficulty of discerning catch-up protein growth: dissected tissue weights may not differ between control and refed pigs, but subsequent chemical analysis can reveal differences in the chemical composition of these tissues (Vanschoubroek *et al*, 1965), for example, at equal dissected lean mass, refed pigs' lean may contain more protein and water and less energy than lean from control pigs.

The experiment described below sought to clarify the short-term response to refeeding after a period of feed restriction. Pigs were given individual levels of feed restriction, determined by their feed intake on a particular day, rather than imposing a standard degree of restriction which would, by definition, have retarded the growth of some pigs more than others.

MATERIALS AND METHODS

Large White female pigs were weaned at 14 days of age and 3.84 (±0.121) kg live weight into tiered cages. After seven days on *ad-libitum* intake of the early-weaning diet (Table 1.1, Section 1) 35 pigs, now weighing 4.68 (±0.140) kg live weight, were transferred to individual cages fitted with nipple drinkers and troughs designed to minimise spillage.

Room temperature was gradually reduced from 27°C (at 14 days of age) to 24°C (at 70 days of age). Between 21 and 25 days of age all pigs were fed to appetite on the early-weaning diet. "To appetite" feeding involved the provision of three discrete "meals" per day, the

quantity allowed being increased slightly when the previous "meal" had been consumed entirely.

At 25 days an initial slaughter group of 4 pigs was killed and four different feeding regimes were imposed on the 31 pigs remaining (Table 2.3).

TABLE 2.3: Experimental design

	Group:			
	I	II	III	IV
Total number of pigs	14	9	6	6
Slaughtered, 25 days of age	4	-	-	-
Intake, 25-40 days	A	R1	A	R2
Slaughtered, 40 days of age	4	3	-	-
Intake, 40-55 days	A	R1	R3	R2
Slaughtered, 55 days of age	3	3	3	3
Intake 55-70 days	A	A	A	R2
Slaughtered, 70 days of age	3	3	3	3

A feeding to appetite, three times daily

R1 daily intake restricted to intake at 25 days of age

R2 daily intake restricted to 200 g

R3 daily intake restricted to intake at 40 days of age

Between 25 and 40 days of age, 16 pigs were fed to appetite thrice daily on the early-weaning diet (10 pigs in Group I, 6 pigs in GroupIII), 9 pigs were restricted to their feed intake at 25 days of age (Group II) and 6 pigs were restricted to 200 g early-weaning diet per day (Group IV). It was decided that 200 g day^{-1} represented a level of feed intake likely to result in weight stasis or liveweight loss when offered from 25 days of age onwards. At 40 days, 7 pigs were slaughtered (4 from Group I, 3 from Group II). Between 40 and 55 days of age 6 pigs continued to be fed to appetite (Group I), 6 pigs continued to be

restricted to their intake at 25 days (Group II), 6 pigs were restricted to their intake at 40 days (Group III) and 6 pigs continued to be restricted to 200 g day^{-1} (Group IV). At 55 days three pigs from each of the four Groups were slaughtered. Between 55 and 70 days of age 9 pigs were fed to appetite (Groups I, II and III) while 3 pigs continued to be restricted to 200 g day^{-1}. At 70 days the remaining 12 pigs were slaughtered.

Slaughter procedure comprised administration of a lethal dose of sodium pentabarbitone, removal of gut contents and mincing of the whole empty body, twice through a 13 mm plate and once through a 5 mm plate. Dry matter was determined by oven-drying fresh mince at 95°C to constant weight. Samples for chemical analysis were freeze-dried and milled. Gross energy (GE) was determined by adiabatic bomb calorimetry, nitrogen by Kjeldahl digestion, and lipid by use of the equation: Lipid = (GE - 0.1475 N)/0.0393 (Whittemore *et al*, 1976).

Within treatment Groups, carcass compositions of slaughtered pigs were used in linear regression analysis to derive the relative proportions in the live weight at slaughter of empty body, water, nitrogen, lipid and ash. These proportions were then used to estimate the carcass compositions of pigs not slaughtered. Daily gains in live weight and body components, daily feed intakes, daily feed intakes relative to mean live weight, and carcass compositions were examined by analysis of variance with the Genstat V, Mark 4.01 programme (Lawes Agricultural Trust, 1977).

RESULTS

Changes in live weight are shown in Figure 2.10. The companion Figure 2.11 gives the same information for pigs killed at 70 days of age

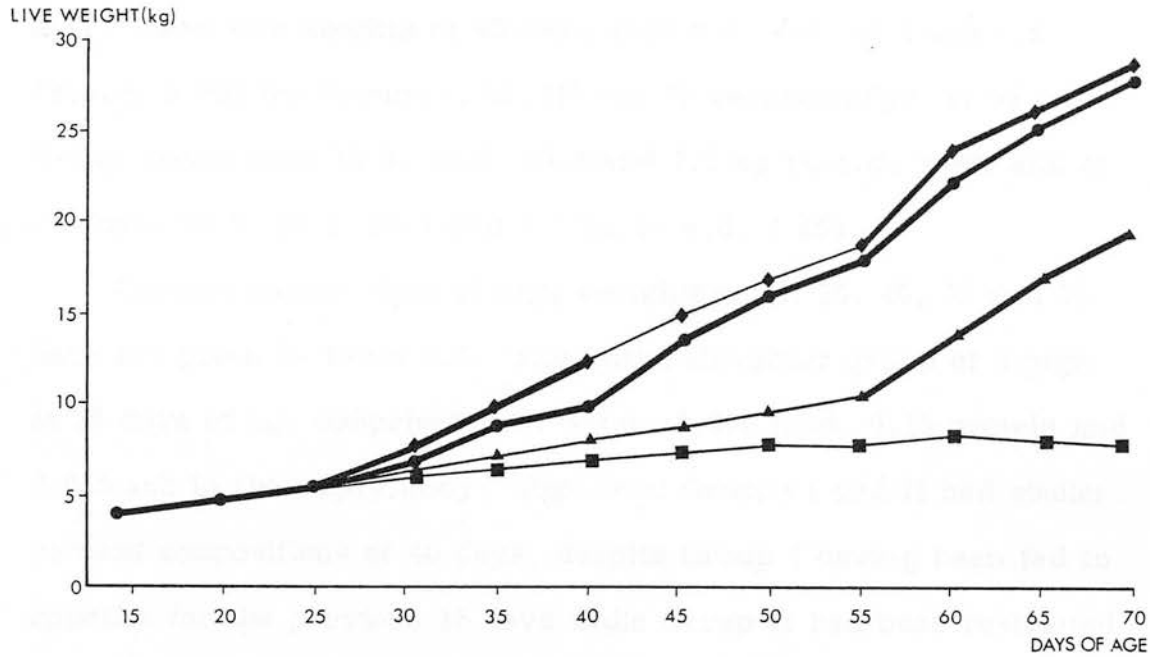


FIGURE 2.10: Changes in live weight (kg) between 14 and 70 days of age of female pigs fed to appetite (Group I, ●), severely restricted and refed (Group II, ▲), mildly restricted and refed (Group III, ◆) and severely restricted (Group IV, ■). All pigs.

Thin lines denote periods of feed restriction, thick lines represent feeding to appetite.

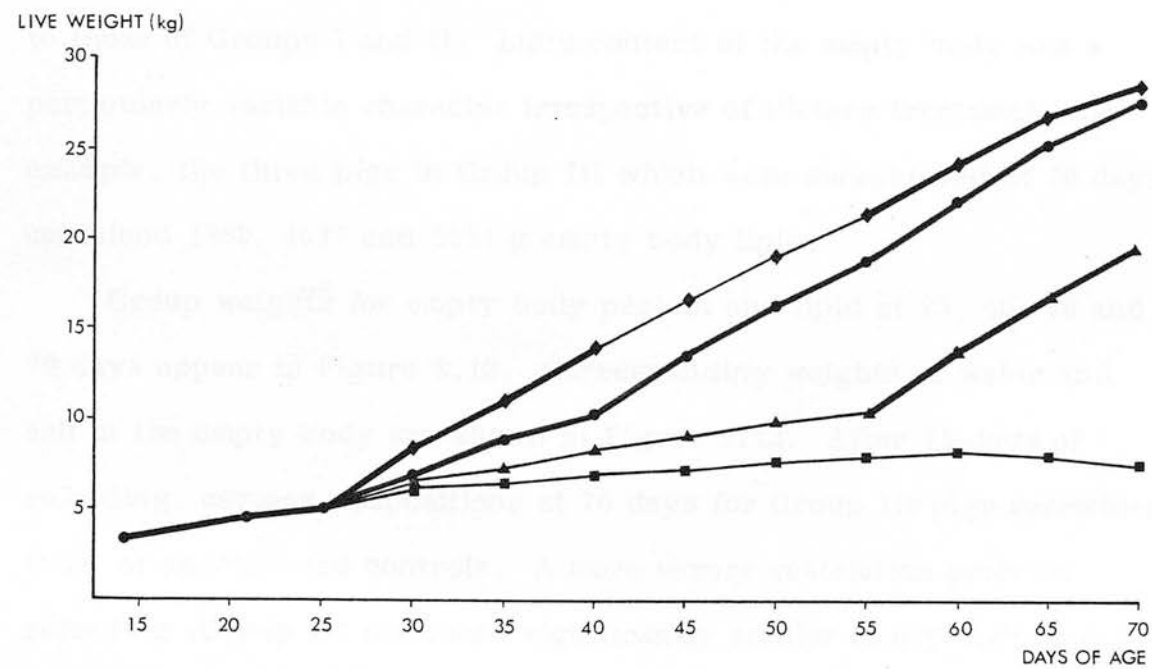


FIGURE 2.11: Changes in live weight (kg) between 14 and 70 days of age of female pigs fed to appetite (Group I, ●), severely restricted and refed (Group II, ▲), mildly restricted and refed (Group III, ◆) and severely restricted (Group IV, ■). Pigs slaughtered at 70 days only.

only. Mean live weights at 40 days were 9.8, 8.0, 12.2 and 6.8 (s.e.d. 1.05) for Groups I, II, III and IV respectively; at 55 days Group means were 18.0, 10.5, 18.4 and 7.7 kg (s.e.d. 1.80) and at 70 days, 27.8, 19.5, 28.7 and 7.7 kg (s.e.d. 3.65).

Carcass compositions of pigs slaughtered at 25, 40, 55 and 70 days are given in Table 2.4. The initial slaughter group of 4 pigs at 25 days of age comprised 0.74 water, 0.065 lipid, 0.15 protein and 0.035 ash in the empty body. Pigs from Groups I and II had similar carcass compositions at 40 days, despite Group I having been fed to appetite for the previous 15 days while Group II had been restricted to their 25-day intake. By 55 days of age severely-restricted pigs in Groups II and IV had significantly less mass of empty body and body components than their appetite-fed contemporaries in Group I ($P < 0.01$). Mildly-restricted pigs in Group III (held to their 40-day intakes for the preceding 15 days) were found to have carcass compositions intermediate to those of Groups I and II. Lipid content of the empty body was a particularly variable character irrespective of dietary treatment, for example, the three pigs in Group III which were slaughtered at 70 days contained 1989, 4037 and 5051 g empty body lipid.

Group weights for empty body protein and lipid at 25, 40, 55 and 70 days appear in Figure 2.12. Corresponding weights of water and ash in the empty body are shown in Figure 2.13. After 15 days of refeeding, carcass compositions at 70 days for Group III pigs resembled those of appetite-fed controls. A more severe restriction prior to refeeding (Group II) produced significantly smaller empty body and chemical component masses at 70 days than those of Groups I and III. At this final slaughter age, pigs fed 200 g day^{-1} for 45 days (Group IV) weighed 0.28 of appetite-fed controls and their empty bodies contained only 0.024 lipid.

TABLE 2.4: Empty body composition at 25, 40, 55 and 70 days of age of appetite-fed, restricted, and restricted and refed female pigs (all weights in grammes)

Days of age	Group: I	II	III	IV	s.e. of difference and level of significance
25 (n = 4)					
Live weight	4978.0				
Empty body weight	4410.0				
Water	3259.0				
Lipid	286.5				
Protein	660.0				
Ash	153.3				
40 (n = 7)					
Live weight	9550.0	8044.0			2334.70
Empty body weight	8525.0	6827.0			2058.90
Water	5624.0	4888.0			1329.50
Lipid	757.2	434.5			403.09
Protein	1685.6	1225.0			330.44
Ash	346.9	252.0			67.64
55 (n = 12)					
Live weight	17095.0	8963.0	15183.0	7216.0	2495.90 **
Empty body weight	15318.0	8422.0	14267.0	6967.0	2201.10 **
Water	10159.0	6172.0	9521.0	5104.0	1421.30 **
Lipid	1516.0	428.1	1293.4	260.5	430.92 *
Protein	2961.9	1419.4	2777.5	1295.0	353.25 **
Ash	563.7	317.3	534.1	305.2	72.30 **
70 (n = 12)					
Live weight	27750.0	19467.0	28733.0	7718.0	2495.90 **
Empty body weight	25333.0	17233.0	26500.0	7213.0	2201.10 **
Water	16922.0	11649.0	17359.0	5240.0	1421.30 **
Lipid	2992.9	1846.5	2914.3	171.1	430.92 *
Protein	4269.4	3035.0	4653.1	1364.4	353.25 **
Ash	850.9	545.0	996.3	316.6	72.30 **

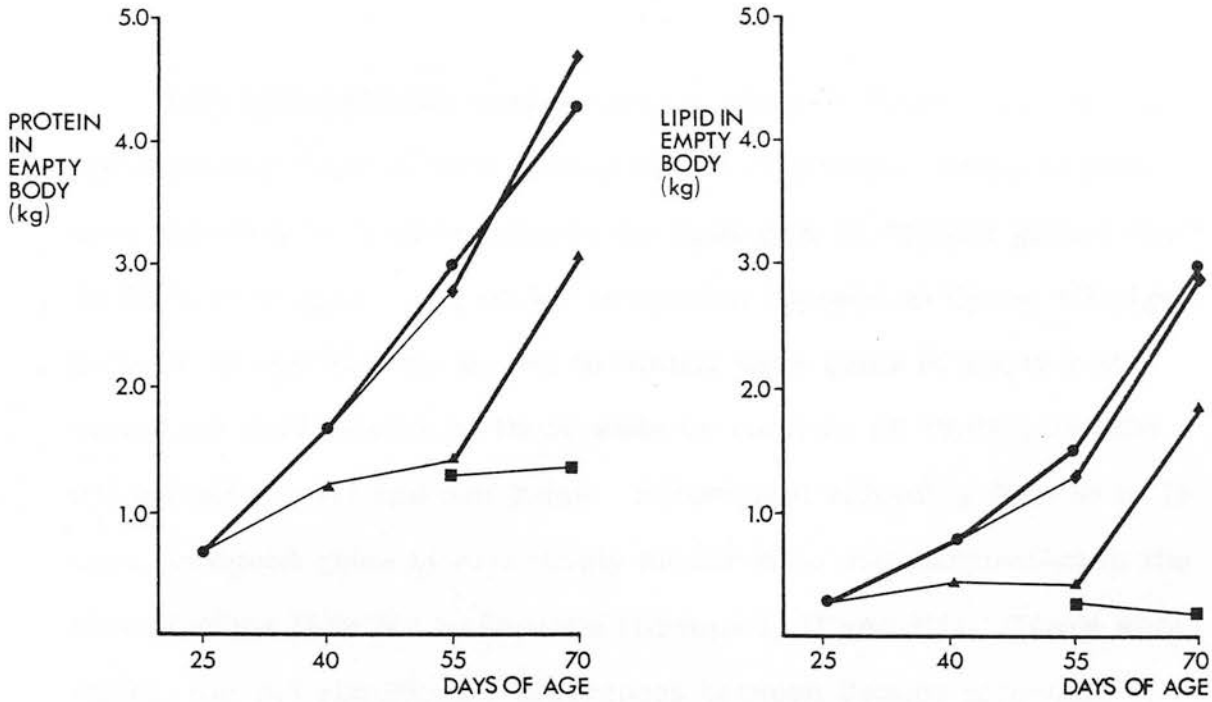


FIGURE 2.12: Protein and lipid in the empty body at 25, 40, 55 and 70 days of age of female pigs fed to appetite, severely restricted and refed, mildly restricted and refed and severely restricted.

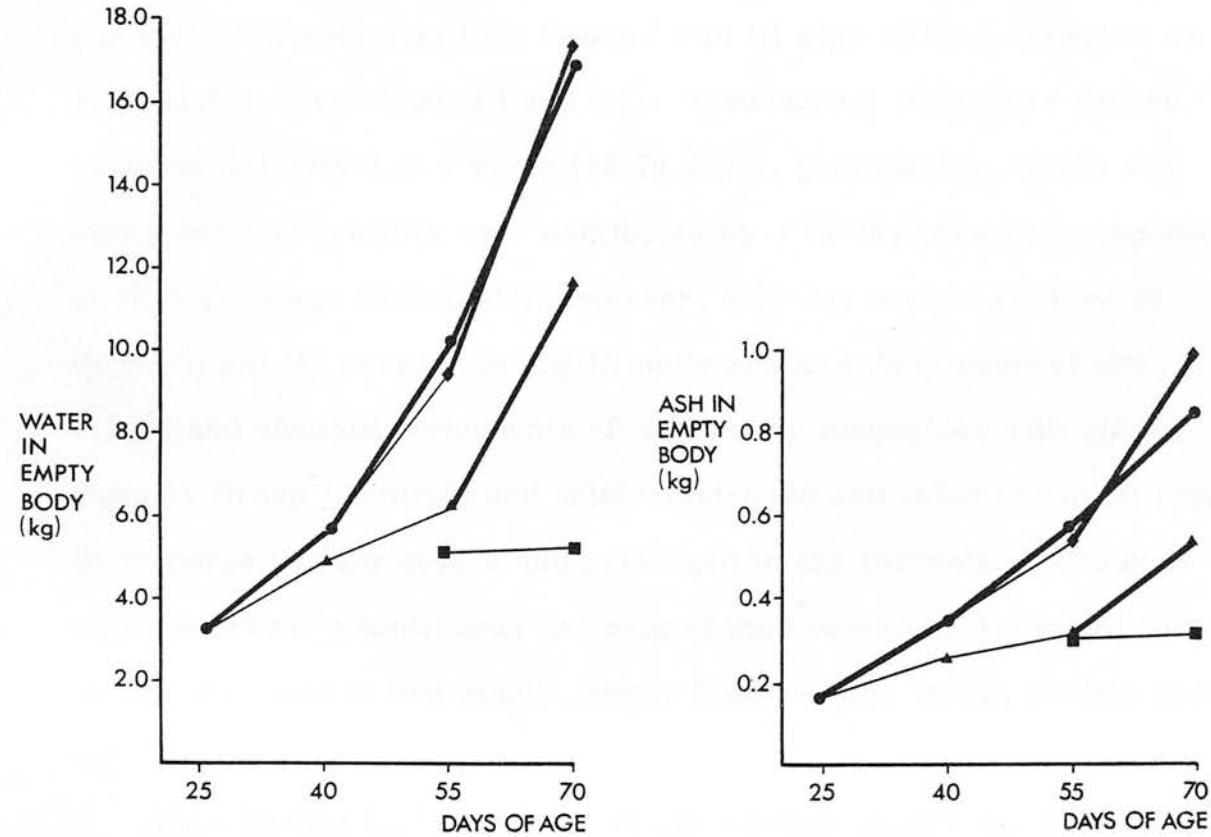


FIGURE 2.13: Water and ash in the empty body at 25, 40, 55 and 70 days of age of female pigs fed to appetite, severely restricted and refed, mildly restricted and refed and severely restricted.

Daily gains of body components are given in Table 2.5. During the second 15 days of their 30-day intake restriction, Group II pigs were narrowly in positive balance for lipid gain (0.99 lipid gained day^{-1}, 40-55 days of age). The milder restriction imposed on Group III pigs between 40 and 55 days served to reduce daily gains of empty body, water and lipid relative to those made by controls ($P < 0.01$), but did not curtail protein and ash gains. Subsequent refeeding from 55 to 70 days produced gains of remarkably similar mass and composition in the three Groups then fed to appetite (Groups I, II and III). There were slight, but not significant, differences between Groups according to previous dietary intake: for refed Groups, empty body weight comprised a lower fraction of live weight (0.80 and 0.87 for Groups II and III vs 0.95 for Group I controls), while Group II pigs deposited less water per unit of protein gain than Group I and III pigs (3.0 : 1, Group II vs 5.7 and 5.4 : 1 for Groups I and III). Considering daily gains for the experimental period as a whole (25-70 days), gains in live weight and empty body components were unaffected by a 15-day restriction imposed at 40 days of age (Group III), however, a 30-day restriction from 25 days (Group II) resulted in significantly reduced daily gains of live weight and chemical components ($P < 0.001$) by comparison with gains made by Group I controls and mildly-restricted and refed Group III pigs. In response to their severe and prolonged intake restriction, Group IV pigs underwent a continuous draining of lipid reserves concurrent with small daily gains in live weight, empty body weight, water, protein and ash.

Feed intakes kg^{-1} mean live weight between 25 and 40, 40 and 55, 55 and 70 and 25 and 70 days are shown in Figure 2.14. Refed pigs ate the same per kg mean live weight as control contemporaries of greater

TABLE 2.5: Daily gains of live weight, empty body weight, water, lipid, protein and ash between 25 and 40, 40 and 55, 55 and 70 and 25 and 70 days of age by appetite-fed, restricted, and restricted and refed female pigs (all weights in grammes)

Days of age	Group: I	II	III	IV	s.e. of difference and level of significance
25-40 (n = 7)					
Live weight	314.0	191.0			38.90 ***
Empty body weight	274.4	154.5			32.70 **
Water	204.6	104.1			19.31 **
Lipid	30.7	9.3			7.19 *
Protein	63.3	36.4			10.19 *
Ash	12.4	6.4			1.89 **
40-55 (n = 9)					
Live weight	532.0	169.0	414.0		65.80 ***
Empty body weight	440.1	129.2	331.7		44.00 **
Water	296.1	102.3	228.4		24.59 **
Lipid	48.1	1.0	29.7		16.11 ***
Protein	81.8	16.7	61.8		10.78 **
Ash	13.1	5.1	10.2		1.70 **
55-70 (n = 12)					
Live weight	595.0	495.0	481.0	-23.0	116.10 **
Empty body weight	563.7	396.2	419.5	-25.8	87.50 ***
Water	381.9	225.9	262.3	-21.8	61.70 **
Lipid	87.4	83.9	67.4	- 7.5	33.70
Protein	67.4	75.4	48.2	- 3.2	12.62 **
Ash	14.8	8.2	15.9	- 1.0	4.53 *
25-70 (n = 12)					
Live weight	504.0	313.0	491.0	42.0	68.00 ***
Empty body weight	463.7	277.1	457.9	45.4	58.00 ***
Water	302.8	180.8	289.8	31.7	38.30 ***
Lipid	60.0	34.1	56.2	- 3.7	13.75 **
Protein	79.9	51.5	83.6	13.0	7.66 ***
Ash	15.0	8.4	17.6	3.0	1.79 ***

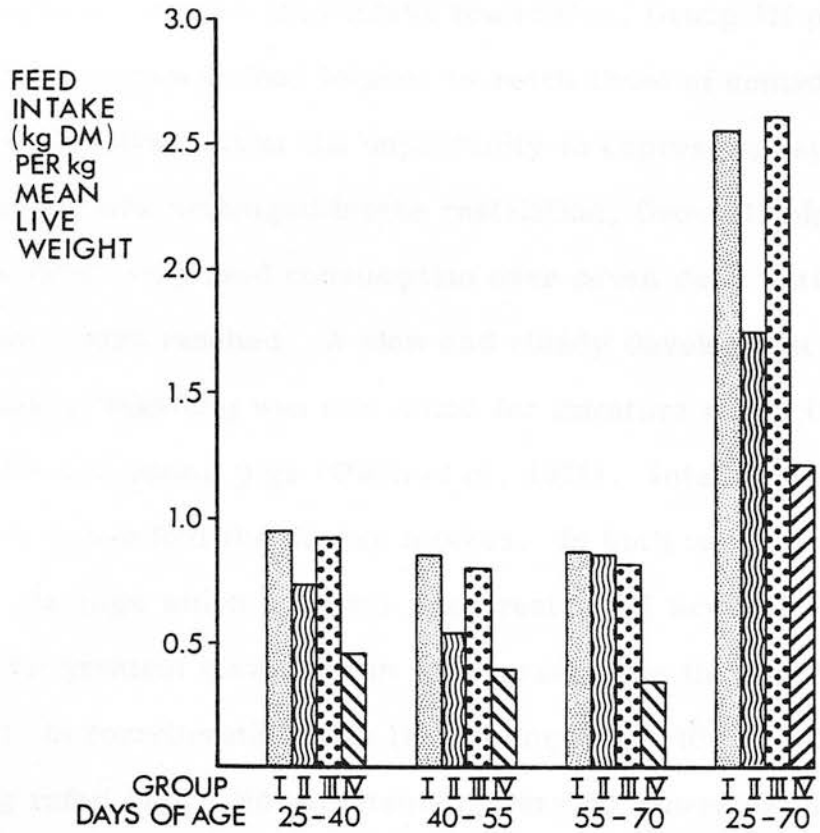


FIGURE 2.14: Feed intake per kg mean live weight between 25 and 40, 40 and 55, 55 and 70 and 25 and 70 days of age by female pigs fed to appetite, severely restricted and refed, mildly restricted and refed and severely restricted.

live weight, and also ate the same per kg mean live weight as control pigs at equal live weight but a younger age.

DISCUSSION

Voluntary feed intake during rehabilitation

On removal of their mild intake restriction, Group III pigs rapidly increased their feed intakes to match those of control pigs of the same age. When given the opportunity to express appetite after a more severe and prolonged intake restriction, Group II pigs gradually multiplied their daily feed consumption over seven days until plateaux intake levels were reached. A slow and steady development of feed intake during refeeding was also noted for immature sheep (Drew and Reid, 1975) and young pigs (Owen *et al*, 1971). Intake plateaux were between 4- and 9-fold the 25-day intakes. In both refed Groups (II and III), the pigs which ate least when restricted were the pigs which realised the greatest elevations in feed intake once the restriction was rescinded, in corroboration with the findings of Wyllie and Owen (1978b) for young refed pigs. Notwithstanding very considerable increases in feed consumption by realimented pigs, the control pigs' daily feed intakes were not significantly exceeded, either in absolute terms (1345, 903 and 1374 g DM day^{-1} for Groups I, II and III respectively between 55 and 70 days, s.e.d. 167.6) or on a mean live weight basis (Figure 2.14), and despite the fact that the diet offered was fairly high in energy (15.8 MJDE kg^{-1} DM). Control pigs, always fed to appetite, appeared to eat less food relative to mean body weight as the trial progressed. However, if feed intakes are expressed on a metabolic body weight basis then they actually rose from $0.113W^{0.75}$ (25 to 40 days) to $0.156W^{0.75}$ (55 to 70 days).

Enhanced voluntary feed intakes, to the extent of surpassing feed intakes of age controls, have not usually been observed in refed pigs (Vanschoubroek *et al*, 1965; Wyllie and Owen, 1978b) or chickens (Wilson and Osbourn, 1960; Auckland and Morris, 1971; Washburn and Bondari, 1978). There were two exceptions to this generalisation for pigs: Cole *et al* (1968) reported significantly greater feed intakes by refed pigs following intake restriction to 50 kg live weight ($P < 0.05$), while Ratcliffe and Fowler (1980) found elevated feed intakes subsequent to an early intake restraint (birth to 15 kg live weight), an effect which was more pronounced for female refed pigs than for male pigs.

Effect of restriction on empty body composition

Differences in carcass composition between appetite-fed (Group I) and severely-restricted pigs (Groups II and IV) were not significant until 55 days of age, when the restricted pigs had undergone 30 days of intake limitation. At 55 days, slaughtered pigs from Groups I and IV contained 0.099 and 0.037 lipid in the empty body respectively; corresponding Group means for empty body protein were 0.193 and 0.186. The comparative stability of empty body protein under diverse feeding regimes has been noted elsewhere (Elsley, 1964; Méndez, 1966; Goenaga and Carden, 1978).

Recovery of lipid reserves, depleted after weaning at 14 days of age, was protracted. If the lipid content of suckled pigs is taken as being 0.15 of the empty body (Manners and McCrea, 1963; Whittemore *et al*, 1978), then this content was reduced to 0.065 by 25 days of age and increased gradually to 0.118 by 70 days. Hence, even after 55 days of appetite feeding, weaned pigs had not regained their pre-weaning body lipid reserves. Concurrent with this moderate rate of lipid deposition were daily protein gains which compared favourably with

values in the literature for pigs of similar age and live weight:

Protein deposition rate ($g\ day^{-1}$)	Source
82 (0.178 of empty body gain)	6 pigs from Groups I and III, 25 to 70 days of age at a mean live weight of 16.6 kg
62	calculated from equation in Thorbek (1975)
70	Jones, Hepburn and Boyne (1960)
73	Hencken, Freese and Lenkeit (1963) Stein and Gebhardt (1971)
81	Ludvigsen and Thorbek (1959)

Influence of restriction and refeeding on the rate of liveweight gain

There was a 15-day difference between Groups I and II in age at 10 kg live weight and a 13-day difference in age at 19 kg live weight. Further, a 6.9 kg discrepancy in empty body weight at 55 days was enlarged to 8.1 kg at 70 days. Failure by refed pigs to catch-up in live weight with control pigs is not unique to the present trial. Lodge, Sarkar and Friend (1977), in common with the present experiment, slaughtered restricted and refed pigs after a fairly brief period of realimentation. Pigs were restricted from birth (by limiting access to the sow and to creep feed) to 35 days of age and were realimented between 35 and 70 days. Refed pigs did not diminish the controls' weight advantage. The authors reported an acceleration in protein synthesis rate in the livers of refed pigs, but the latters' overall rate of protein deposition between 35 and 70 days was not significantly higher than that of age controls.

Change in live weight over time was strikingly parallel for Group II pigs during appetite feeding (55 to 70 days) and for control pigs,

whether of the same age (Group I, 55 to 70 days) or of the same weight (Group I, 40 to 55 days) (Figures 2.10 and 2.11). This analogy in growth curves was also true for restricted and refed Japanese quail (*Coturnix*) and their continuously-fed contemporaries (Morse and Vohra, 1971), regardless of the duration of the intake restraint (Figure 2.15). The intervention of sexual maturity at around 50 days of age produced a "flattening off" of the controls' growth curve such that they slowed down in their rate of growth, whereas refed quail continue to increase in body weight at greater ages (mechanism (ii), Eckles and Swett, 1918). Although Auckland and Morris (1971) claimed compensatory growth in turkeys following a protein restriction to 6 weeks of age, a difference in live weight at 6 weeks of 325 g was hardly reduced during adequate feeding and was still 308 g at 10 weeks and 277 g at 20 weeks.

Pigs given adequate protein after protein intake restriction over the first 11 weeks of life had a growth curve parallel to that of unrestricted age controls (Atinmo, Baldijao, Pond and Barnes, 1976). In a similar experiment, Pond, Yen and Lindvall (1980) fed both lean-type pigs (Hampshire x Yorkshire) and obese-type pigs (Duroc x Yorkshire) on a diet containing 120 g protein kg^{-1} until 56 days of age (Figure 2.16). When offered a diet containing 180 g protein kg^{-1} *ad-libitum* from 56 days, the lean-type refed pigs did not reduce the difference in age at a particular live weight between themselves and lean-type control pigs, that is, no catch-up liveweight gains were observed. It might have been anticipated that of the two genotypes, lean-type pigs would have shown the greatest response to diet change-over, presumably having suffered the greater deprivation during protein restriction. Japanese quail selected for faster (lean) growth rate

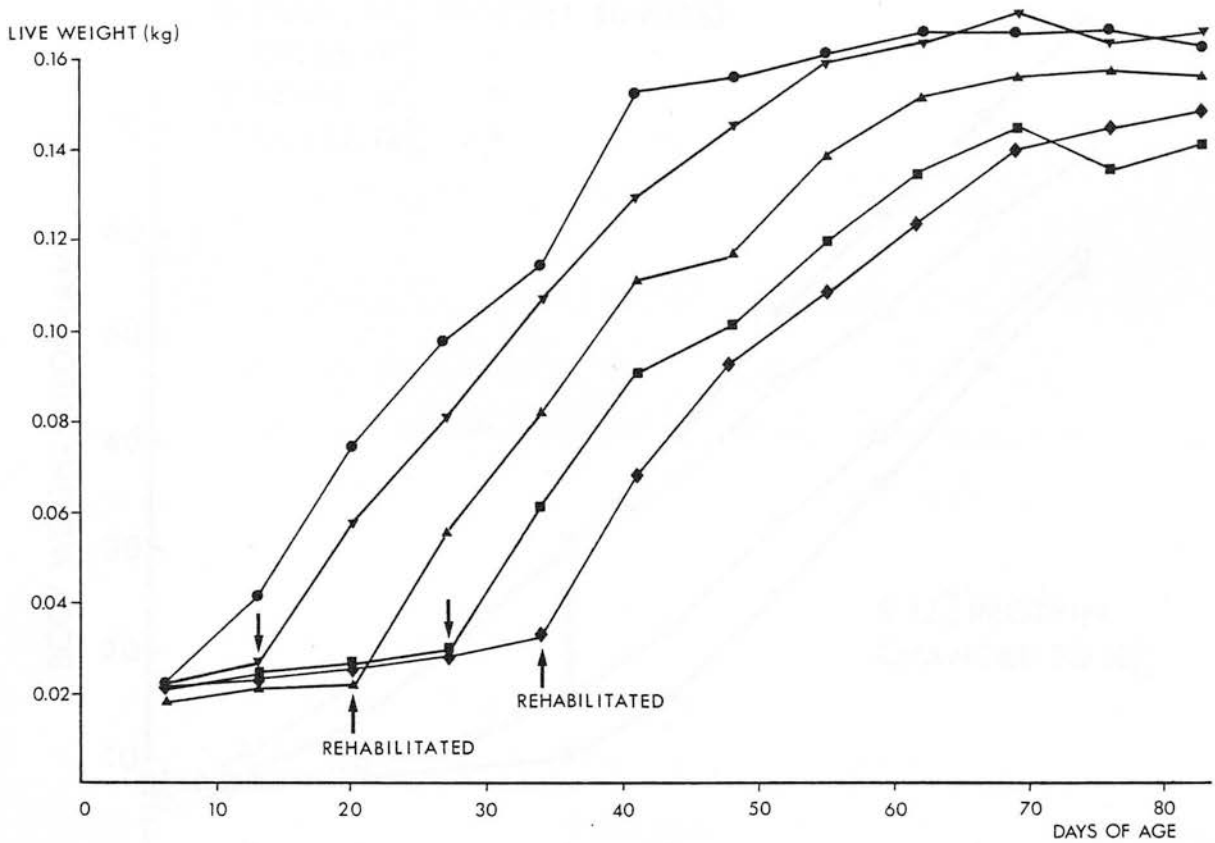


FIGURE 2.15: Changes in live weight (kg) between 6 and 83 days of age of Japanese quail (*Coturnix*) fed to appetite (●) and restricted for 7 (▼), 20 (▲), 27 (■) or 34 (♦) days and realimented (Morse and Vohra, 1971).

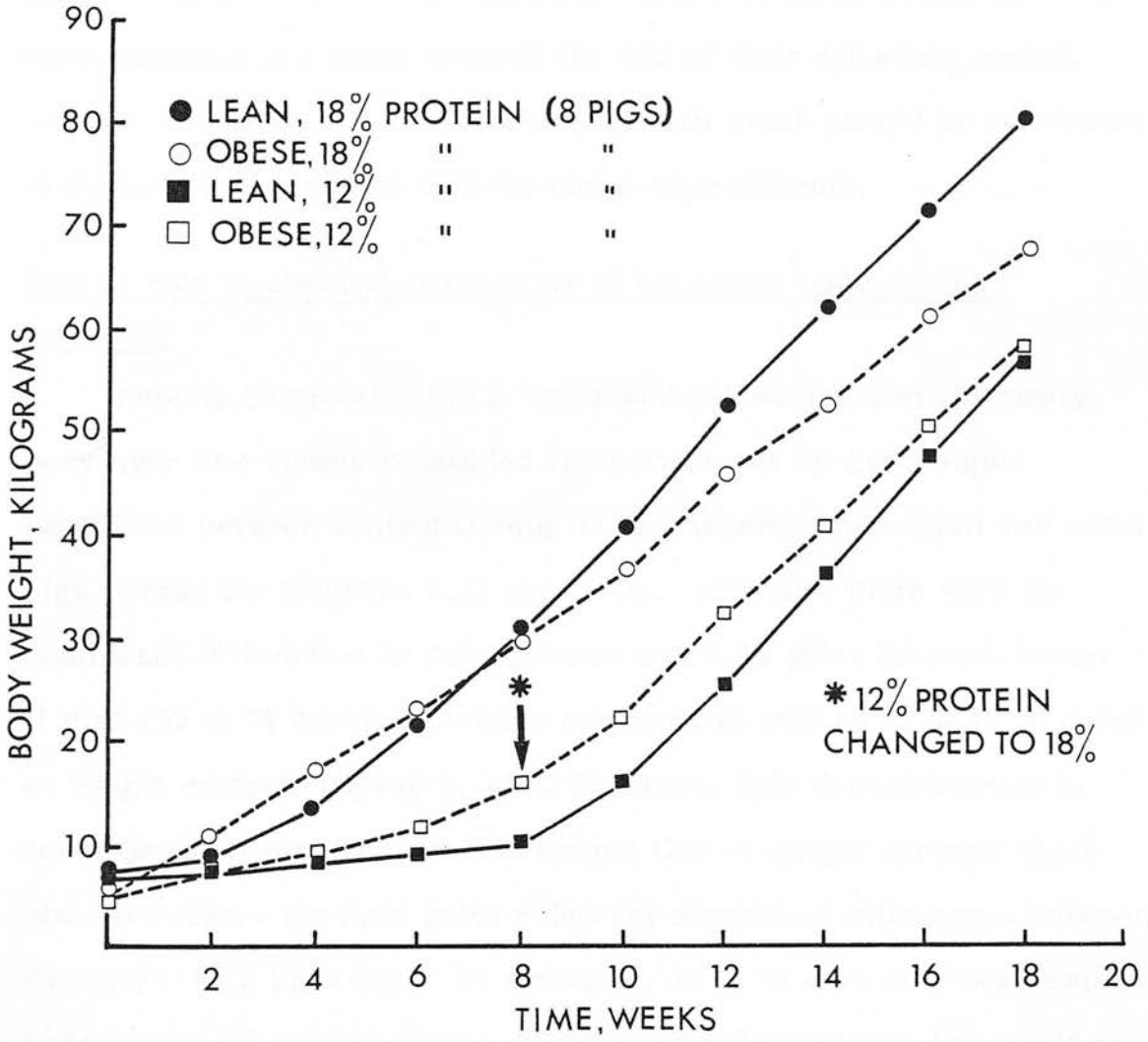


FIGURE 2.16: Changes in live weight (kg) between birth and 18 weeks of age of lean-type and obese-type pigs fed a high-protein diet throughout or restricted in protein intake to 8 weeks and realimented (Pond, Yen and Lindvall, 1980).

gleaned more benefit subsequently in growth impulsion terms from a period of protein restriction (0 to 14 days of age) than unselected quail (Marks, 1978). Obese-type pigs (Pond *et al*, 1980) appeared to make compensatory gains towards the end of their refeeding period, but this may be an illusory catch-up growth which should be attributed to deceleration of growth rate by obese-type controls.

Rate of gain in chemical components of the empty body during refeeding

Increase in protein, lipid, water and ash contents of the empty body over time closely resembled the pattern set by live weight: parallelism between control (Group I) and severely-restricted and refed pigs (Group II) (Figures 2.12 and 2.13). Although there were no significant differences in daily protein and lipid gains between Group II pigs (55 to 70 days) and either age controls (Group I, 55 to 70 days) or weight controls (Group I, 40 to 55 days), lipid deposition rate in refed Group II pigs appeared to exceed that of weight controls (high standard errors for lipid gains ruled out significant differences between Groups): 84 g lipid day^{-1} for Group II, 55 to 70 days at a mean empty body weight of 12828 g versus 48 g lipid day^{-1} for Group I pigs, 40 to 55 days at a mean empty body weight of 11922 g.

The tissues implicated in catch-up growth remain controversial. The type of restriction imposed (feed level, protein alone or energy alone) and the severity of the restriction (slower weight gain, weight stasis or weight loss) will condition the response obtained on refeeding. First, where animals have lost weight, or have been restricted for protein only, their regrowth frequently contains a high proportion of water and protein (pigs: Zimmerman and Khajarern, 1973; Hogberg

and Zimmerman, 1976, and Wyllie and Owen, 1976a; lambs: Ørskov *et al*, 1976), particularly in the offal fraction (Reid *et al*, 1968). Ørskov *et al* (1976) fed a low-protein diet to lambs until 28 kg live weight, and then offered a high-protein diet restricted in quantity to intakes recorded for lambs of equal live weight fed *ad-libitum* on the high-protein diet throughout. Immediately after the diet change-over refed lambs made very rapid gains in live weight which, by serial slaughter, were found to include a large water component. The authors proposed that the protein deposited following protein restriction has a greater water-binding capacity than usual. In support of this suggestion, Drew and Reid (1975) noted that the first 5 kg of empty body gain by immature sheep subsequent to substantial weight loss was almost exclusively water and protein. However, gains additional to this first 5 kg comprised protein and lipid gains akin to (and not significantly different from) those of continuously-fed sheep of the same age; some of the refed sheep were fed *ad-libitum*, others were limited to the intakes of continuously-fed weight controls. The liveweight gain of turkeys subjected to protein restriction for the first 6 weeks of life and then realimented to 20 weeks of age contained exactly the same proportions of water and protein as the liveweight gain of control turkeys (Auckland and Morris, 1971).

Second, a constraint to feed allowance or to energy alone seems to promote a high proportion of lipid in the regrowth (pigs: McMeekan, 1940, Lister and McCance, 1967, Fowler and Livingstone, 1971; cockerels: Wilson and Osbourn, 1960; sheep and rats: Meyer and Clawson, 1964; rats: Stewart, 1974, Lau, Flaim and Ritchey, 1976, Harris and Widdowson, 1978, Panemangalore *et al*, 1978). Enhanced lipid deposition occured in existing adipose cells (Hirsch and Han, 1969;

Lee, Kauffman and Grummer, 1973) and not in new adipose cells formed during realimentation. In their 15 days of feeding to appetite, Group II pigs made daily empty body gains comprising 0.21 lipid, 0.57 water and 0.19 protein. Over the same time period, Group I controls made daily gains containing 0.16 lipid, 0.68 water and 0.12 protein, indicating the tendency for the regrowth in this experiment to be "fatter" and "drier" than growth in contemporaries.

Implications of severe intake restriction for body protein reserves

Comparison of Table 2.5 and Figure 2.12 for severely-restricted pigs in Group IV (200 g day^{-1}) reveals two contradictory estimates of protein growth: a negative increment for daily protein gain between 55 and 70 days (Table 2.6) as opposed to an increase in empty body protein mass between the pigs slaughtered at 55 days of age and those slaughtered at 70 days. This conundrum points to the shortcoming of regression analysis for prediction of live animal composition from slaughtered animal composition when small numbers of pigs are used and growth is not radically different to zero. Even after 45 days of severe intake restriction it was not possible to discern whether or not protein mass underwent depletion. The fact that the pigs used in this experiment were both young and female may have rendered them particularly resistent to erosion of protein reserves. Widdowson (1976) subjected animals of different ages to periods of starvation and found young animals lost less protein than adults. In response to feed restriction, young female rats lost more lipid and less protein than young male rats (Widdowson, 1976). Lister and McCance (1967) fed very low quantities of food to pigs in order to maintain live weights of 5 to 6 kg for a year and found a very much higher survival rate for female restricted pigs than in their male counterparts; that the males

died of infections and heart failure is indicative of considerable protein loss, to the extent of invalidating the immune system and the electrolyte balance in cardiac muscle. On refeeding, female pigs made swifter recoveries than male pigs. Refed female rats were also shown to make an earlier, faster and more complete recovery from an intake restriction applied between birth and 21 days of age (Williams and Hughes, 1975).

Efficiency of feed utilisation for growth according to dietary treatment

Having established that refed pigs did not consume more food than unrestricted controls, the possibility of improved efficiency of utilisation of the same food remained. Table 2.6 gives efficiencies of protein and energy utilisation for Groups I, II and III, calculated as the ratio of protein and energy deposited (g day^{-1}) to the quantity of digestible crude protein and digestible energy consumed (g DCP day^{-1} and MJ DE day^{-1}). Restricted pigs were less efficient than control pigs of the same age in their conversion of dietary protein and energy to protein and energy in the empty body (Group II, 25 to 55 days and Group III, 40 to 55 days, $P < 0.05$), although control and mildly-restricted Group III pigs did not differ in their utilisation of dietary energy.

Refed pigs converted feed to gain with the same efficiency as control pigs of the same age (55 to 70 days) and same live weight (40 to 55 days). A significantly reduced efficiency of protein utilisation by Group III pigs relative to Group II pigs can be attributed to the unexpectedly low efficiency exhibited by Group III pigs, rather than the distinct enhancement of efficiency for Group II pigs.

Over the trial as a whole, dietary treatment had no bearing on efficiency of conversion of dietary protein and energy to chemical components, the length and severity of feed restriction notwithstanding.

TABLE 2.6: Efficiency of utilisation of dietary protein and energy by appetite-fed and restricted and refed female pigs between 25 and 40, 40 and 55, 55 and 70 and 25 and 70 days of age

Days of age	Group: I	II	III	s.e. of difference and level of significance
25-40				
Protein utilisation[1]	0.705	0.537	-	0.0505 *
Energy utilisation[2]	0.379	0.248	-	0.0387 *
40-55				
Protein utilisation	0.526	0.261	0.443	0.0879 *
Energy utilisation	0.326	0.041	0.232	0.0674 *
55-70				
Protein utilisation	0.243	0.427	0.169	0.0800 *
Energy utilisation	0.233	0.354	0.202	0.0565 NS
25-70				
Protein utilisation	0.412	0.527	0.396	0.0485 NS
Energy utilisation	0.290	0.337	0.269	0.0399 NS

[1]Protein deposited (g day^{-1})/protein consumed (g DCP day^{-1})

[2]Energy deposited (MJ day^{-1})/energy consumed (MJ DE day^{-1})

SUMMARY

Catch-up growth, involving an enhanced rate of protein deposition, did not take place on removal of a post-weaning feed restriction. Previously-restricted pigs did not consume more food than controls, nor did they utilise the same feed more efficiently. Empty body gains did not differ significantly in composition to those of age controls, but may have contained more lipid than empty body gains made by controls of the same weight but younger age. If the rate of protein synthesis was accelerated in certain parts of the empty body (for example, the liver)

during refeeding, this was masked by similar overall rates of protein gain for refed and control pigs.

D. GROWTH AND BODY COMPOSITION OF YOUNG ENTIRE MALE PIGS FED TWO DIETS OF DIFFERING INGREDIENT COMPOSITION

[see Appendix 2.3]

In its examination of the part played by diet composition in post-weaning growth this experiment was particularly concerned with possible nutritional constraints on growth rate, mediated through nutrient quality as distinct from nutrient supply *per se*. Entire male pigs were chosen for this trial as being those animals most likely to respond favourably to higher quality diets.

MATERIAL AND METHODS

Twenty-eight littermate pairs of entire male Large White pigs were weaned at 14 days of age and a mean live weight of 5.59 (±0.139) kg. They were housed in individual wire-mesh cages with free access to water. One pig from each pair was offered diet 'S' and the other offered diet 'B' (Table 2.7), both diets being in the form of a dry meal. Pigs were fed twice daily to appetite. Live weight was measured weekly until pigs reached 25.0 (±0.06) kg live weight when 15 pairs were slaughtered. Intestinal contents were removed and the whole empty body minced. Samples for chemical analysis were freeze-dried and milled, while the dry matter (DM) content was determined by oven-drying freshly-minced material to constant weight. Gross energy (GE) was determined by adiabatic bomb calorimetry, nitrogen by Kjeldahl digestion, and lipid by use of the equation: Lipid = (GE - 0.1475 N)/ 0.0393 (Whittemore *et al*, 1976).

TABLE 2.7: Dietary composition and chemical analysis of experimental diets for young boar pigs

	Diet†: 'S'	'B'
Ingredient (kg t^{-1} fresh weight)		
Barley	109	500
Wheat	250	87
Flaked maize	265	100
Soya bean (extracted)	224	255
Fat premix (60 g kg^{-1})	60	22
Herring meal	50	-
Meat and bone meal	19	-
Avotan 20	2.0	2.0
Choline chloride	0.4	0.4
Salt	1.2	2.2
Limestone	2.0	5.6
Dicalcium phosphate	13.6	22.4
Minimix PG 360	3.5	3.5
Dry matter (g kg^{-1} fresh weight)	878.1	878.7
Chemical composition (g kg^{-1}DM)		
Gross energy (MJ)	18.85 (±0.068)	18.25 (±0.076)
Crude protein	234.56 (±1.744)	213.50 (±3.475)
Lipid	50.31	25.00
Ash	61.62	60.77
Crude fibre	60.55	62.22
DE (MJ) i) from ingredients	16.00	15.00
ii) from diet specification	16.40	15.20
iii) from TDN	16.60	15.00
DE (MJ) : CP (g) ratio	0.068	0.070

†Super Kwik Wean Meal ('S', Super) and Kwik Wean Meal ('B', Basic), RHM Agriculture Ltd.

Diets 'S' and 'B' contained respectively (g kg^{-1} DM):

Calcium 1.012, 1.004; Phosphorus 0.833, 0.842; Salt 0.376, 0.386; Methionine + cystine 0.750, 0.641; Lysine 1.217, 1.057; Available lysine 1.226, 1.053; Available phosphorus 0.614, 0.581; Tryptophan 0.435, 0.353; Threonine 0.881, 0.759; Isoleucine 1.110, 0.998.

The chemical compositions of pigs when weaned at 21 days of age was predicted by means of the following regression equations (Whittemore, Taylor and Crooks, 1974):

Empty body weight (EBW) (g)	= 0.923 live weight (g) + 140 (±0.0223)
Water (g)	= 0.647 EBW (g) + 177 (±0.0223)
Nitrogen (g)	= 0.0241 EBW (g) - 6.47 (±0.00155)
Lipid (g)	= 0.174 EBW (g) - 172 (±0.0226)
Ash (g)	= 0.0201 EBW (g) + 31 (±0.00429)
Gross energy (MJ)	= 0.0103 EBW (g) - 6.20 (±0.00084)

Determined levels of crude protein (CP) were 235 and 214 g kg^{-1} DM for diets 'S' and 'B' respectively; calculated energy values were 16.0 and 15.0 MJ DE kg^{-1} DM.

Daily liveweight gains and feed intakes for individual pigs were calculated by regression of accumulated mass on time; differences in growth and performance between pigs offered the two diets were assessed by paired t-test for comparison of the difference between means.

RESULTS

Growth rates and feed intakes for pigs offered diets 'S' and 'B' are given in Table 2.8.

Incidence of scouring was low on both diets. Weekly weights are illustrated in Figure 2.17.

Pigs offered diet 'S' grew more rapidly, ate 8.9 kg less in total than pigs given diet 'B', and reached 25 kg live weight an average of

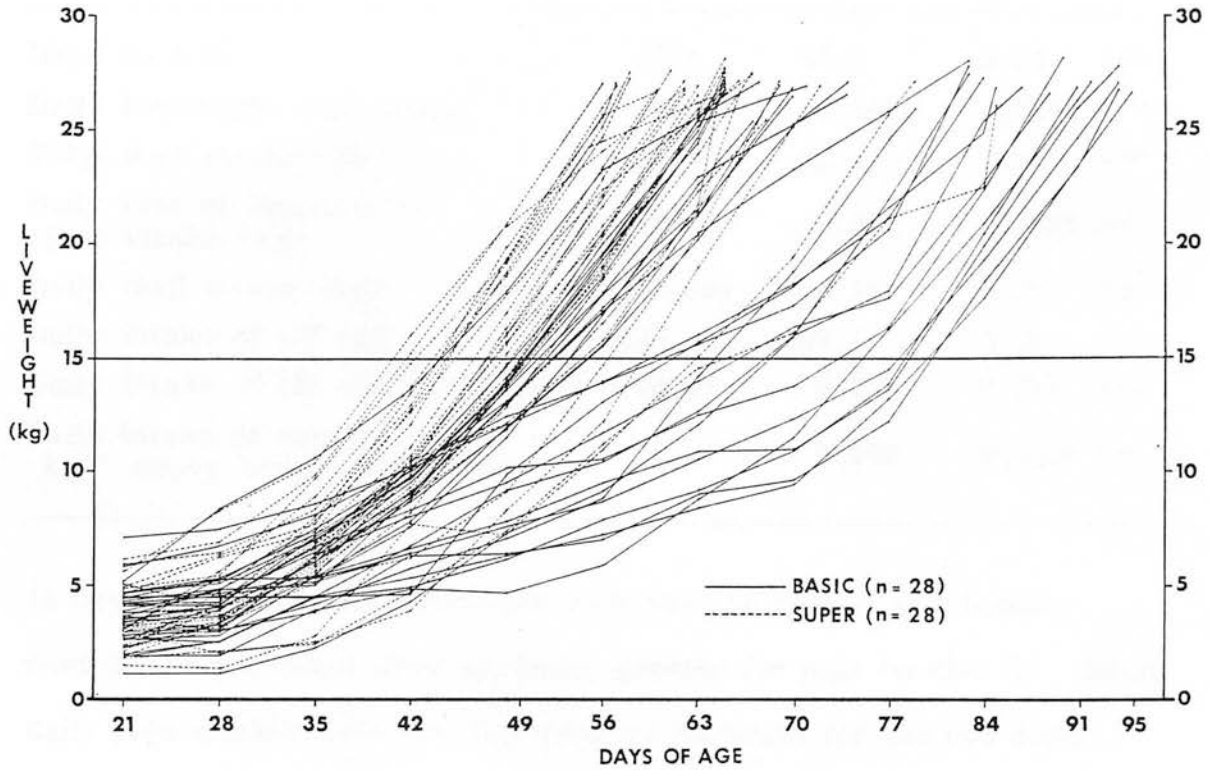


FIGURE 2.17: Weekly weights and liveweight gains (kg) of young entire male pigs fed two diets of differing nutrient quality.

TABLE 2.8: Performance of entire male pigs from 5.59 to 25.0 kg live weight

	Diets: 'S'	'B'	s.e. of difference and level of significance	
Days on test	43.6	57.6	2.23	***
Daily liveweight gain (kg)	0.475	0.349	0.0190	***
Total feed intake (kg)	33.6	42.5	1.72	***
Daily rate of increase in feed intake (kg)	0.032	0.022	0.0018	***
Daily feed intake (kg)	0.804	0.756	0.026	NS
Daily intake of CP (g)	160.4	139.1	3.74	***
Daily intake of DE (MJ)	10.94	9.78	0.259	***
Daily intake of energy kg^{-1} empty body weight (MJ)	0.475	0.448	0.0160	NS

14 days sooner. Daily liveweight gain and the rate at which daily feed intake increased were markedly greater for pigs on diet 'S'. Mean daily feed intakes were not significantly different for the two diets, although the higher nutrient density of diet 'S' resulted in significantly enhanced intakes of crude protein and digestible energy.

An increase in daily liveweight gain was associated with a decrease in total feed consumed: total feed intake (kg) = 70.4 (±2.82) - 80.5 (±6.90) daily liveweight gain (kg). This reflects the relative digestibilities of the two diets, together with the additional maintenance costs accruing from slower growth on diet 'B'. The relationship between total feed intake (Y,kg) and days on test (X) varied with nutrient density of the diet such that the slope for diet 'S' had a lower gradient and greater constant when compared to the slope for diet 'B':

Diet 'S' $Y = 0.407\ X + 16.0$ (± 0.0615) (± 2.70)

Diet 'B' $Y = 0.620\ X + 6.8$ (± 0.0860) (± 5.03)

Pigs fed diet 'B' showed far greater variation in performance, notably with respect to time taken to reach 25 kg live weight (s.d. diet 'S' 6.5, diet 'B' 11.2). Daily feed intake (X,kg) was a good predictor of daily liveweight gain (Y, kg) for pigs fed diet 'S' [$Y = 0.626\ (\pm 0.0838)X - 0.033\ (\pm 0.0658)$] but not for pigs fed diet 'B' [$Y = 0.092\ (\pm 0.1677)X + 0.278\ (\pm 0.1258)$].

There was no discernible effect of diet on chemical composition of the empty body at 25 kg live weight (Table 2.9). Pigs given diet 'S' deposited considerably more protein daily than pigs given diet 'B' (63.3 vs 54.9 g), notwithstanding the similarity in efficiencies of protein and energy utilisation on the two diets.

TABLE 2.9.: Chemical composition of the empty body of 25 kg entire male pigs and their efficiency of utilisation of nutrients

	Diets: 'S'	'B'	s.e. of difference and level of significance
Empty body weight (kg)	22.54	21.61	0.171 ***
Empty body protein (kg)	3.52	3.49	0.056 NS
Empty body lipid (kg)	2.73	2.72	0.101 NS
Energy in empty body (MJGE)	190.5	189.3	3.93 NS
Daily empty body gain (kg)	0.393	0.327	0.0106 ***
Daily protein retention (g)	63.3	54.9	1.95 ***
Daily energy retention (MJGE)	3.26	2.80	0.098 ***
Protein retained (g day^{-1})/ protein consumed (g day^{-1})	0.398	0.386	0.0148 NS
Energy retained (MJ day^{-1})/ DE consumed (MJ day^{-1})	0.302	0.292	0.0077 NS

DISCUSSION

Total feed intake to 25 kg live weight was lower for pigs given diet 'S'. Of the extra 8.9 kg eaten by pigs offered diet 'B', between 5 and 6 kg can be attributed to increased maintenance costs over the extended growth period. In theory, diet 'S' possessed no advantage in terms of DE : CP ratio (0.068 vs 0.070 for diet 'B'), however, in practice it seems likely that the improved performance achieved on this diet stemmed from its higher nutrient quality, greater digestibility and its stimulatory effect on rate of increase of feed intake. The last of these may be ascribed to an enhanced palatability of diet 'S'. Positive influence of "palatability" on feed intake by pigs, so awkward a factor to quantify, has recently been questioned by Fowler (1981). Nevertheless, greater variation in feed intakes of young pigs was observed when diets of lower nutrient density were offered (Holub, 1969).

At 25 kg live weight all pigs contained 12.4% empty body lipid. Only in response to weaner diets of narrower energy : protein ratio do young pigs achieve a swift recovery of lipid reserves to their pre-weaning level of around 15% of the empty body (Campbell, 1977; Whittemore *et al*, 1978, Section 2, Part A). Both diets fell within the recommended range of energy : protein ratio for optimum protein and lipid deposition (Clawson, Blumer, Smart and Barrick, 1962; Wilson and Leibholz, 1979) and indeed, protein retentions on diets 'S' and 'B' (63.3 and 54.9 g day^{-1} respectively) were somewhat higher than retentions measured in other slaughter trials using pigs of similar weight (Likuski, Bowland and Berg, 1961; Whittemore and Illius, 1974; De Goey and Ewan, 1975).

Differences in growth rate between pigs fed diet 'S' and those fed diet 'B' were most apparent in the first stage of the trial, there

being 12 days' difference in time taken to reach 15 kg live weight (diet 'S' 28 days and diet 'B' 40 days on test, s.e. = 2.1, $P < 0.001$). However, this discrepancy was reduced subsequent to 15 kg live weight: the time taken to grow from 15 to 25 kg live weight differed by only 3 days between treatments (diet 'S' 15 days and diet 'B' 18 days, s.e. 0.9, $P < 0.01$). It would appear that it was particularly in the early stages of post-weaning growth that the greater nutrient density of diet 'S' was of most benefit to the young pig's digestive physiology. Inclusion in diet 'S' of extra wheat, flaked maize (cooked starch) and animal protein brought about a reduction in fibre content of 0.0028 and increase in digestible energy content of 0.067 relative to diet 'B'; this relatively minor improvement in nutrient density and quality was responsible for a profound difference in growth rate during the 14 days following weaning. An interaction is implicated between nutrient density, palatability (readiness to achieve high feed intake) and digestibility for the weaner diets studied.

The experiment described in Section 2C failed to detect an acceleration in protein gain subsequent to a period of intake restriction. However, evidence from rat and human studies suggest adaptation of protein metabolism to counterbalance protein supply : enhanced efficiency of protein utilisation induced by a period of protein shortage is shown to persist when protein supply returns to an adequate level, leading to catch-up protein gains. This would be of practical relevance if a fluctuating supply of protein to pigs produced a more efficient overall utilisation of the protein source, and if the destination of extra protein deposited in the empty body was an edible fraction.

SECTION III

Compensatory Nitrogen Retention in Growing Pigs

INTRODUCTION

A substantial body of evidence attests the occurrence of a change in protein metabolism during periods of protein deprivation, and the persistance of this modified metabolic state into at least the early stages of realimentation for protein.

Limited data are available for protein synthesis and turnover rates in the growing pig, but no material has been produced which deals exclusively with the catch-up mechanism, and for the latter it is necessary to consult the comprehensive information available for growing rats, and to a lesser extent, malnourished and rehabilitated infants. In the case of human infants, circumstances beyond the control of the experimenter are likely to have imposed the intake restriction, and in the majority of cases restriction will be for both energy and protein rather than for protein alone. The rat provides an acceptable model for the pig, particularly when the two species are compared for protein synthesis rate on a metabolic body weight basis and at similar proportions of maturity. For example, Millward (1979) quoted a daily whole body turnover rate in the 116 g rat of 25.4 g kg^{-1} $BW^{0.75}$ while Garlick, Burk and Swick (1976) using the same techniques with 76 kg pigs produced a value of 26.6 g $kg^{-1}BW^{0.75}$ day^{-1}.

Preferred methods of assessment of protein turnover rate involve continuous infusion, over a period of 6 to 8 hours, of a labelled amino-acid such as leucine or tyrosine (Simon, Münchmeyer, Bergner, Żebrowska and Buraczewska, 1978; Reeds and Lobley, 1980). In pigs, protein breakdown rate should be calculated as the difference between protein synthesised per unit time and protein deposited per unit time in order to avoid the problems of re-utilisation of amino-acids (Nishizawa, Shimbo, Hareyama and Funabiki, 1977) and non-random

uptake of isotope (Millward, 1979) which beset the direct measurement of breakdown rate. Humans, rats and rabbits have the advantage to the experimenter of excreting 3-methyl hisidine as the only end-point of histidine metabolism, and output of this compound can be used as an index of muscle protein breakdown rate (Milne and Harris, 1978).

Changes in protein turnover during protein deprivation

Garlick (1980) stated that changes in nitrogen retention rate could be achieved by either an increase in protein synthesis rate or a decrease in protein breakdown rate. More is known about the kinetics of protein synthesis than those of protein degradation (Mayer, Burgess and Russell, 1980). During normal growth, a 60 kg pig might deposit over 100 g of protein daily, or between 0.25 and 0.33 of the daily quantity of protein synthesised (Garlick, Burk and Swick, 1976; Edmunds, Buttery and Fisher, 1978). A similar ratio of protein deposited to protein synthesised was obtained for the growing rat; growing chicks deposited almost half of their daily synthetic output (Lewis, Boorman and Buttery, 1976), although this value may have been estimated at a lower proportion of mature size. Protein synthesis rate is most rapid in the young animal (Perry, 1974) and declines with advancing age, this decline being more pronounced in skeletal muscle than in the liver (Garlick *et al*, 1976). Breakdown rate also decreases over time, but with a slower decay rate. At maturity, synthesis rate is still marginally in excess of breakdown rate (Millward, 1979). The entire male synthesises protein at a more rapid rate than the female (Waterlow and Stephen, 1968).

Animal experiments have revealed a reduction in whole body protein turnover consequent upon chronic protein deficiency (Waterlow and Stephen, 1967; Garlick, Millward, James and Waterlow, 1975).

In malnourished children, both protein synthesis and protein breakdown rates in the whole body had decreased by 0.40 (Golden, Waterlow and Picou, 1977); protein-deprived weanling rats underwent a reduction in rate of muscle protein synthesis from 0.062 day^{-1} (0.062 of muscle protein replaced daily) to 0.027 day^{-1} (Waterlow and Stephen, 1968). The malnourished children studied by Golden *et al* (1977) appeared to have a lower maintenance requirement for protein: when given 0.6 g protein kg^{-1} day^{-1} malnourished children retained one-third of protein intake whereas recovered children on the same protein intake were only just in positive nitrogen balance.

Attention has focussed chiefly on the liver and skeletal muscles as principal locations for change in protein turnover rate during a period of inadequate protein supply, notwithstanding the finding of Norton and Walker (1971) that recently-weaned lambs lost most nitrogen from the liver and skin when fed on a nitrogen-free diet. Rats given a protein-deficient diet for 3 days suffered a considerable loss of nitrogen from the body, the greater part of which stemmed from the viscera. It took a more prolonged protein deprivation to commence depletion of the protein store in skeletal muscle (Mendes and Waterlow, 1958; Munro, 1964). The liver, accounting for 0.10 of whole body protein synthesis in the pig and rat (Garlick *et al*, 1975; Garlick *et al*, 1976), seeks to maintain its synthetic rate in the face of protein shortage to preserve its role as an exporter of protein to other tissues. Malnourished rats showed markedly reduced rates of incorporation of labelled amino-acids into muscle protein, but incorporation of such amino-acids into liver protein was maintained or elevated (Waterlow and Stephen, 1966; Munro, 1969). Regulation of liver protein balance is achieved by adjustment of liver protein breakdown rate (Mortimore and Ward, 1976),

rather than by alteration of protein synthesis rate (Garlick, Millward and James, 1973; Roobol and Alleyne, 1974); this leads to a gradual decrease in liver protein mass (Coward, Whitehead and Lunn, 1977). Loss of liver protein, together with protein from plasma and the gastro-intestinal tract, comprises an animal's short-term response to dietary protein shortage (Garlick, Millward and James, 1973). In the mal-nourished state, some of the liver protein synthesised will become enzymes involved in liver gluconeogenesis, catalyzing the utilisation of non-essential amino-acids for energy production (Ichihara and Koyama, 1966; Kaplan and Pitot, 1970).

Muscle mass, particularly in the pig as opposed to the rat, represents the major non-fat energy store in the body (Millward and Waterlow, 1978). Protein-deficient rats underwent a slow wasting of muscle mass (Coward *et al*, 1977), while in rats given a protein-free diet for 100 days, muscle and skin protein contributed 0.80 of the total nitrogen lost (Allison and Wannemacher, 1965). Muscle's potential for protein synthesis is a function of its complement of nuclei (estimated from its DNA content), however, the actual rate of protein synthesis depends on muscle's RNA content and the degree of RNA activity, each of which can vary considerably to accommodate acute and chronic changes in nutritional status (Millward, Nnanyelugo, James and Garlick, 1974c). RNA content of muscle is reduced by shortage of amino-acids and by advancing age (Young and Alexis, 1968; Howarth, 1972).

It is highly likely that skeletal muscle protein turnover rate comes under hormonal control. Protein-restricted rabbits had lowered insulin concentrations, decreased responsiveness to insulin and showed signs of reduced sensitivity to growth hormone, another "anabolic" hormone

(Turner and Munday, 1974; Allen, Ayres, Munday and Turner, 1975). Malnourished children showed an elevation in their level of circulating growth hormone (Ashworth, 1969), which may also be indicative of diminished responsiveness by the tissues. Glucocorticoids are acknowledged to be catabolic in action, suppressing protein synthesis (Goldberg and Goldspink, 1975; Shoji and Pennington, 1977). Nevertheless, the ratio of corticosterone : insulin in the rat was only marginally raised during protein deficiency, suggesting a more complex overall mechanism, and one which differs from that causing muscle protein loss during energy restriction when this ratio increased substantially (Millward, 1979). Protein synthesis rate in trunk muscles is more sensitive to dietary protein changes than protein synthesis rate in limb muscles, reflecting differences between muscles in responsiveness to hormones according to their anatomical location (Preedy, Pain and Garlick, 1980).

Reduction in protein turnover under circumstances of protein shortage may have the additional purpose of saving on energy expenditure. The quantity of energy secured by this process would not be of great importance in human infants, where protein turnover accounts for only 0.05 to 0.09 of total heat production (Golden *et al*, 1977), but would be of more significance in the pig and rat, where protein turnover represents around 0.17 of resting metabolic rate (Garlick *et al*, 1976; Garlick, 1980). Even at nitrogen equilibrium, a 34 kg pig can synthesise 212 g protein day^{-1} (Reeds and Lobley, 1980).

When a normal dietary protein intake is replaced by a low protein diet the nitrogen excreted is reduced in quantity. There are two alternative explanations for this, one, that there is a fall in the overall protein flux rate (where flux rate is the irreversible loss of amino-acids,

Shipley and Clark, 1972), or two, that the proportion of the flux which is excreted decreases (Millward, Garlick, James, Sender and Waterlow, 1976). Early measurements showed flux rate to change very slightly during the first 10 days in which rats were given a low-protein diet (Waterlow and Stephen, 1968). Only after 5 weeks did the flux rate fall to 0.50 of its original value (Waterlow and Stephen, 1967). From more recent experiments (Table 3.1) it has been found that feeding protein-free diets causes a fall in nitrogen excretion which is both more extensive and more rapid. Flux rate was reduced to roughly one-fifth of its original value by 30 days of protein deprivation.

TABLE 3.1: Whole body protein flux rate in rats fed a protein-free diet (Millward, Garlick, James, Sender and Waterlow, 1976)

Initial flux rate:	7.83 gN kg^{-1} day^{-1}
Day	Proportion of initial flux
1	102
2	85
3	81
21	39
30	23

By day 30 of feeding the protein-free diet, muscle protein half-life had increased to 12.1 days (Millward *et al*, 1974; control value 3.1 days), suggesting that the reduction in flux rate during protein deficiency had promoted increased re-utilisation of amino-acids (Nettleton and Hegsted, 1975). Obese adults fed a low-protein, low-energy diet underwent a halving of protein flux rate, from 488 to 228 g protein day^{-1} (Sender, James and Garlick, 1974).

Notwithstanding the more rapid reduction in flux rate following change to a protein-free diet, this mechanism is not sufficiently swift-acting to account for a 0.50 drop in urinary nitrogen output occurring over the 30 hours following a switch of rat diets from one containing 135 g casein kg^{-1} diet to one containing 45 g casein kg^{-1} (Figure 3.1). The activities of six hepatic enzymes were also measured and adhered to the same pattern set by nitrogen excretion: an immediate fall in output or activity when the lower-protein diet was introduced preceded a gradual reduction in output or activity. Thus within 30 hours, nitrogen output and liver enzyme activity were modified from levels commensurate with the higher protein intake to levels appropriate to the lower protein intake (Das and Waterlow, 1974). The authors concluded that "the activity of urea cycle enzymes depends in part on the amount of nitrogen available for excretion after demands for synthesis have been met". Smike (1962) was the first to demonstrate a fall in urea cycle enzyme concentration in response to a protein-free diet of adequate energy, but these measurements were made *in vitro*. Jeffreys and White (1975) fed a similar diet to adult Wistar rats and also produced a reduction in concentration of urea cycle enzymes, conditional on the sex of rat used: female rats underwent this adaptation for dietary carbohydrate in the form of both sucrose and starch, whereas male rats only produced the adaptation if carbohydrate in the diet was in the form of sucrose, providing further evidence of the female's resistance to protein deficiency. It follows that the immediate response to a fall in protein intake can be attributed to the shutting down of the urea cycle and a reduction in the proportion of the flux which is excreted. Persistent protein deprivation will circumscribe protein flux rate.

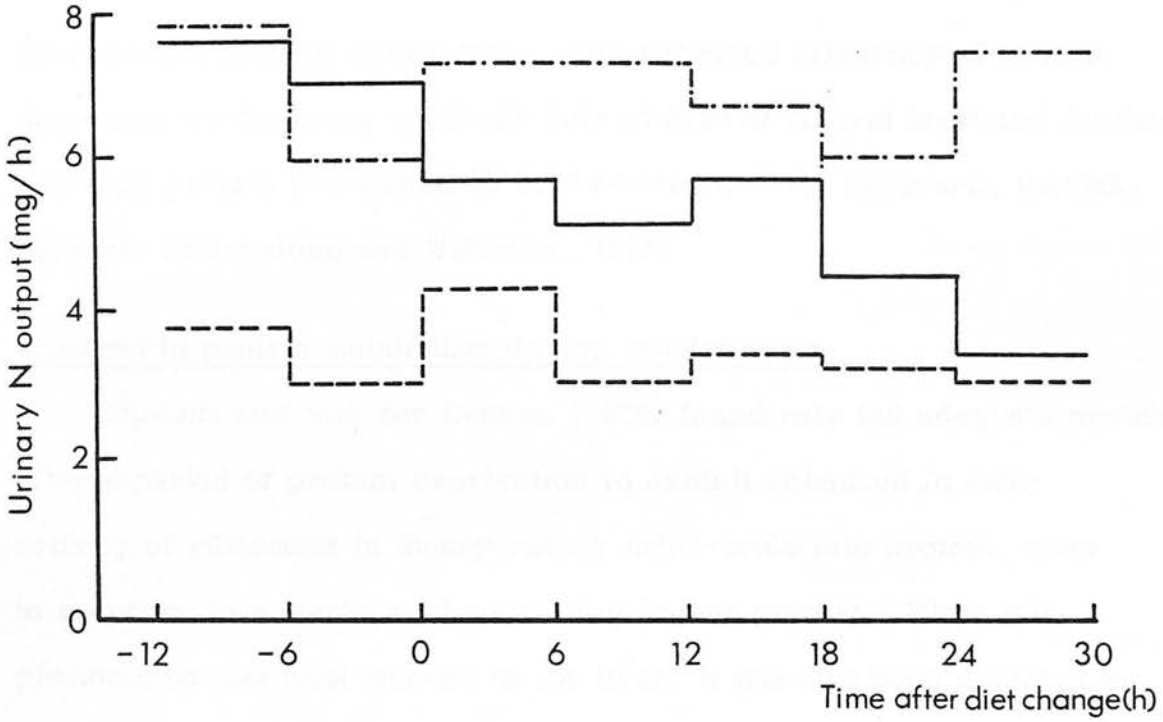


FIGURE 3.1: Urinary nitrogen output of ten rats over 6-hour periods after transfer from a diet containing 135 g casein kg^{-1} (C14) to one containing 45 g casein kg^{-1} (C5) (——) and of one rat maintained throughout on C14 (—.—) and one rat maintained on C5 (---). (Das and Waterlow, 1974.)

Very prolonged protein deficiency, imposed on weaned pigs and lasting for one year, reduced oxygen consumption and therefore metabolic rate (Ablett and McCance, 1969). When extended over several generations, protein deficiency in rats improved efficiency of protein deposition by reducing synthetic rate to 0.50 of control level and further reducing protein breakdown to 0.66 of control level (Millward, Garlick, Stewart, Nnanyelugo and Waterlow, 1975).

Changes in protein metabolism during rehabilitation

Omstedt and von der Decken (1972) found rats fed adequate protein after a period of protein deprivation to exhibit enhanced *in vitro* activity of ribosomes in incorporating amino-acids into protein, even in response to a single meal containing higher protein. While this phenomenon was most marked in the liver, it has also been detected in skeletal muscle (von der Decken and Omstedt, 1972). Subsequent to prolonged protein deficiency in pigs (held at 11 kg live weight for one year), metabolic rate rose rapidly when refeeding commenced (Mount, Lister and McCance, 1963). Table 3.2 details Millward, Nnanyelugo and Garlick's findings: in the first day of refeeding after 30 days on a protein-free diet, weanling rats gained 8 g in body weight but did not increase their muscle weight.

A similar delay in muscle protein response was reported by Mendes and Waterlow (1958), while Roobol and Alleyne (1974) found the initial rise in DNA content to be protracted. The response of liver protein to refeeding was immediate and featured a sharp rise in RNA content (McAnulty and Dickerson, 1974). Also apparent from Table 3.2 is that within 3 days on adequate protein intake, previously-restricted rats had achieved muscle protein growth rates resembling those of normal weanling rats. Protein synthesis rate (and RNA content) in the

TABLE 3.2 Protein metabolism in rat skeletal muscle in response to changes in dietary protein intake (Millward, Nnanyelugo and Garlick, 1974a)

Diet	Day	Muscle protein mass (mg)	Growth rate of muscle protein (day^{-1})	Protein synthesis rate (day^{-1})	Protein breakdown rate (day^{-1})†	$t_{\frac{1}{2}}$
Protein free	30	51	-0.030	0.027 *(±0.009)*	0.057	12.1
High-protein, rehabilitation	1	52	0.043	0.059 *(±0.001)*	0.016	
	3	59	0.049	0.104 *(±0.020)*	0.055	
	8	74	0.068	0.198 *(±0.028)*	0.130	5.3
	14	115	0.061	0.171 *(±0.017)*	0.110	
Weight controls		81	0.050	0.134 *(±0.026)*	0.084	
Age controls		207	0.007	0.078 *(±0.012)*	0.071	

†calculated as synthesis rate - growth rate

muscle tissue had increased, but these rats were able to realise a rapid accumulation of protein by maintaining, in the very early stages of refeeding, the depressed rate of protein breakdown characteristic of the protein deprivation phase. Later in the recovery period, and still consistent with catch-up protein growth, the rates of both protein synthesis and protein breakdown were elevated (Millward *et al*, 1974a); similar increases in protein degradation rate probably occur in recovering infants since excretion of 3-methyl histidine rapidly returns to normal levels during catch-up growth (Rao and Nagabhushan, 1973). Golden *et al* (1977) found protein synthesis and protein breakdown rates in recovering children to be 0.70 and 0.50 higher than rates in recovered children. This implies that unusually rapid protein growth cannot be energetically economic as total protein synthesis greatly exceeds net synthesis.

It has been suggested that re-modelling of contractile cells during growth is associated with some unavoidable wastage, the corollary of which is that during catch-up growth an "anabolic increase" in protein breakdown occurs (Millward, Bates, Laurent and Lo, 1978). In addition, catch-up growth may involve myofibrillar splitting in muscle, as proposed by Goldspink (1970), and this would be accompanied by an acceleration of protein turnover rate; myofibrillar splitting would account for the assertion made by Hogarty and Kim (1980) that muscle fibre numbers, depleted during protein deficiency, are replenished during refeeding.

What happens to protein flux rate during rehabilitation? Table 3.3 gives details of flux rate following the refeeding of rats on a high-protein diet subsequent to 30 days on a protein-free diet.

Having been curtailed by almost 0.80 during protein deficiency, whole body protein flux rate increased gradually over the first 8 days of refeeding.

TABLE 3.3: Whole body protein flux rate in rehabilitated rats (Millward, Nnanyelugo and Garlick, 1974b)

Diet	Days on diet	Body weight (g)		Whole body protein flux ($g\,N\,kg^{-1}\,day^{-1}$)	
			SD		*SD*
Protein-free	30	56	*4*	2.03	*0.38*
High-protein, rehabilitation	1	64	*4*	3.27	*0.34*
	3	78	*6*	5.90	*1.12*
	8	97	*10*	7.12	*0.84*
	14	128	*12*	7.79	*1.33*
Weight controls		110	*6*	8.70	*1.57*
Age controls		205	*6*	5.45	*0.71*

Figure 3.2 illustrates the progress of nitrogen output over 30 hours when rats were switched from a low- to a higher-protein diet, that is, the reverse procedure to that shown in Figure 3.1. Urinary nitrogen output, and the activities of six hepatic enzymes, increased over 30 hours from levels appropriate to the diet containing 45 g casein kg^{-1} to levels commensurate with the diet containing 135 g casein kg^{-1}. However, there was a decided lag, lasting 6 hours, after the diet changeover and before urinary nitrogen output, and liver enzyme activity, began to rise. Similarly, refed infants maintained a low level of nitrogen excretion during early rehabilitation (Figure 3.3).

Why should previously-undernourished animals make catch-up muscle gains when refed? One possibility, mentioned earlier, is that of hormonal control. A second reason could be muscle stretch. In normal growth, muscles are stretched following bone growth (itself under hormonal control) (Stewart, 1972). Malnourished animals would have an abnormal degree of muscle stretch and could gain muscle protein precipitately in order to restore the normal relationship between bone length and muscle mass (Millward, 1979).

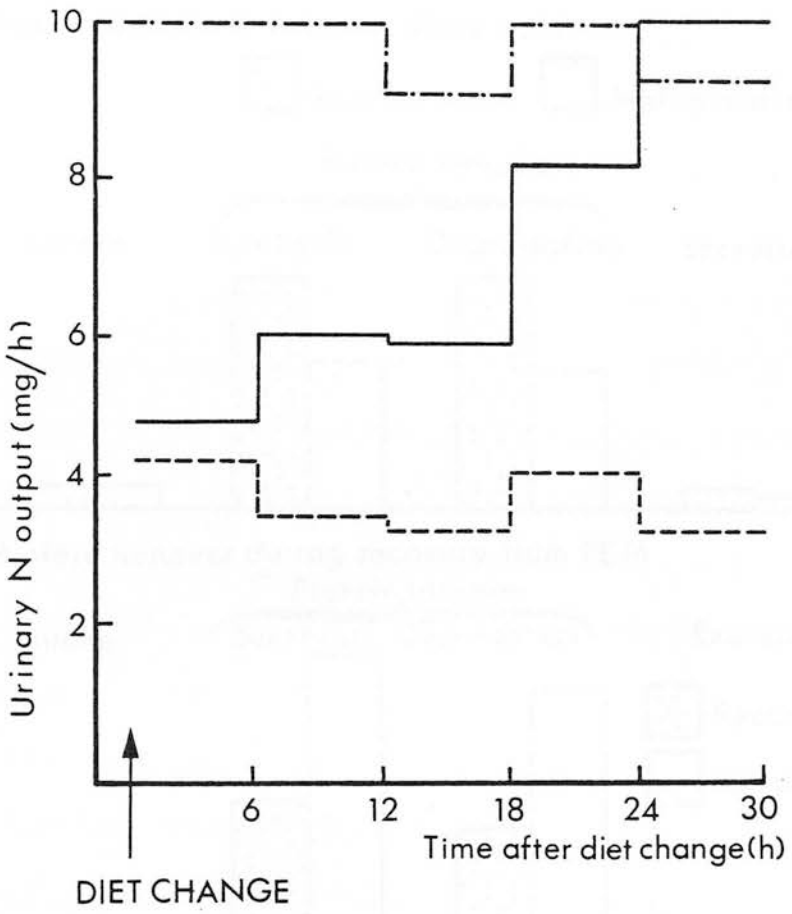


FIGURE 3.2: Urinary nitrogen output in six rats over 6-hour periods after transfer from a diet containing 45 g casein kg^{-1} (C5) to one containing 135 g casein kg^{-1} (C14) (—) and two groups of two rats, one maintained on C5 (---) and the other on C14 throughout (-·-) (Das and Waterlow, 1974.)

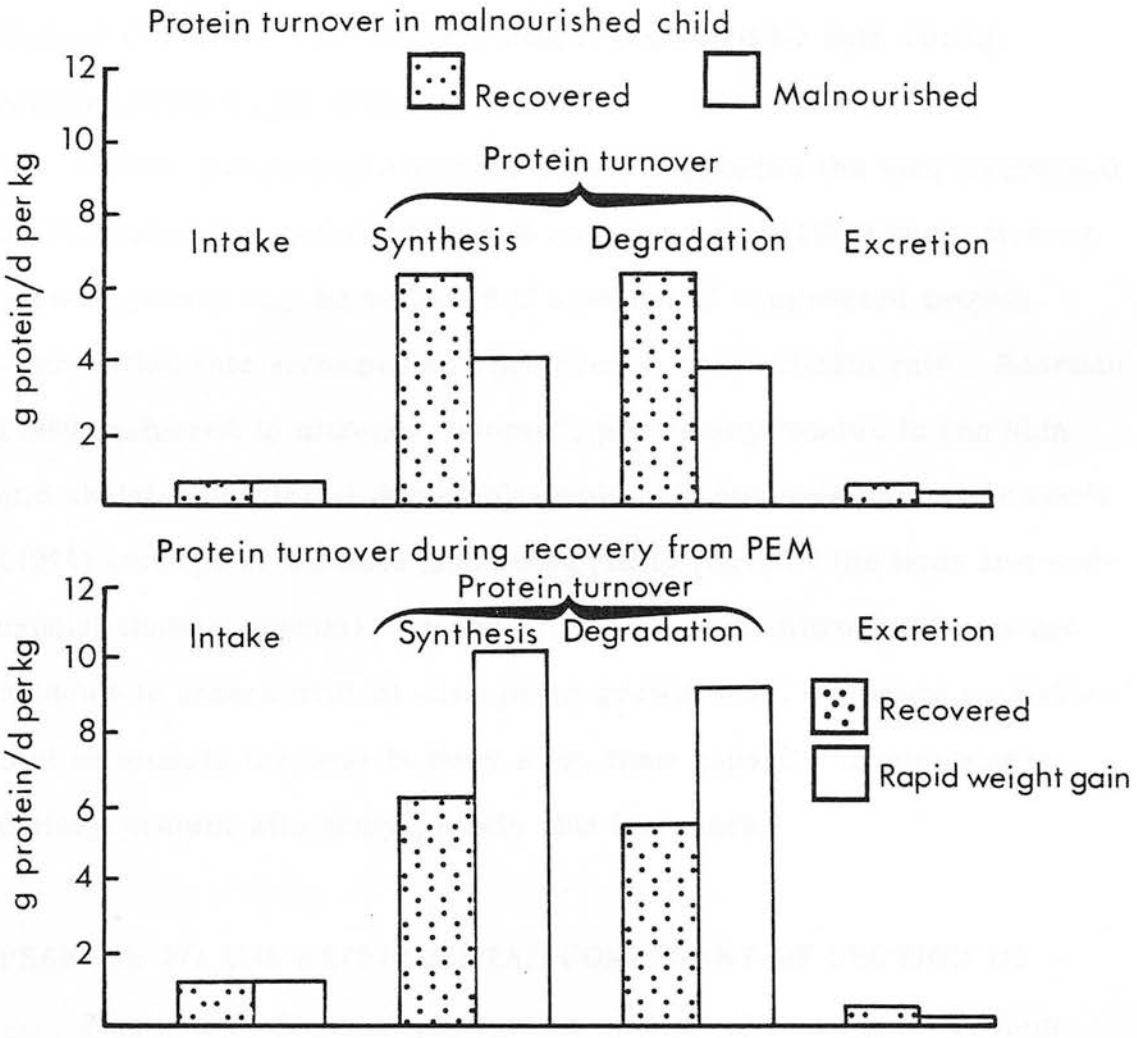


FIGURE 3.3: Whole body protein turnover in malnourished, recovering and recovered children (Picou and Taylor-Roberts, 1969 and Golden, Waterlow and Picou, 1977).

More rapid turnover and accretion rates for protein do not only take place in the liver and skeletal muscle. Čabak, Dickerson and Stanier (1963) traced 0.20 of nitrogen deposited by rats during realimentation to the skin.

Mayer, Burgess and Russell (1980) supported the view expressed by Funabiki, Watanabe, Nishizawa and Hareyama (1976) that catch-up protein growth may be achieved if a period of suppressed protein degradation rate accompanied high protein accumulation rate. Boorman (1980) referred to nitrogen "stores", principally located in the skin and skeletal muscle: a depletable-repletable resource akin to Fowler's (1974) concept of variable lean (comprising parts of the liver and non-crucial skeletal muscle). In the growing animal, nitrogen stores are difficult to assess without disrupting growth rate. It seems probable that as animals increase in body size, their capacity to supplement dietary protein with body protein also increases.

PREFACE TO THE EXPERIMENTAL COMPONENT OF SECTION III

Pigs reared for meat production seldom, if ever, grow protein at a uniformly maximal rate between birth and slaughter. There are phases during which protein growth rate falls below potential, for example, when voluntary food intake is depressed following weaning and changes in stockperson, accommodation or management routine. A further impediment to the achievement of maximum daily protein gain could be imperfect matching of dietary protein supply to pig requirements for protein. While seeking to mitigate such checks to protein growth by improvements in management strategy, it is of practical (as well as biological) interest to investigate the pig's capacity to undergo catch-up protein growth once protein intake ceases to be limiting. If this

capacity is confirmed, then attention can be turned to the quantity of protein required to activate the compensatory mechanism: if pigs recoup lost protein growth on the same protein intake as unrestricted controls then they achieve compensatory protein growth, whereas recovery of lost protein growth reliant on high levels of protein intake constitutes catch-up protein growth. In terms of efficiency of utilisation of food compensation is preferable to catch-up growth.

Also of significance is the time taken to recoup lost protein gain and the anatomical location of enhanced protein deposition during realimentation. Rapidly-growing entire male pigs can reach bacon weight by 120 days after weaning, leaving only limited opportunity for the protracted restoration of lost protein growth; more rapid deposition of protein in inedible offal fulfills the precepts for catch-up protein growth but would not be as advantageous to the pig producer as enhanced protein deposition in muscle. Similarly, account should be taken of the relative overall efficiencies of food utilisation for uninterrupted protein growth and for a period of reduced protein gain followed by catch-up protein growth.

It was decided to investigate the possibility of compensatory growth in pigs using conventional nitrogen balance techniques. By comparison with labelled isotope studies, these techniques have the drawback of revealing nothing of the infuence of nitrogen intake on protein turnover rate or the ultimate destination in the pig's body of retained nitrogen. However, nitrogen balances do permit the measurement of daily nitrogen excretion in urine and faeces in response to different dietary nitrogen intakes. In addition, treatments are easily replicated and expertise in the relevant experimental techniques readily available.

The first experiment sought to establish the existence of a mechanism for compensatory nitrogen retention, while the second experiment further perused the extent and duration of the compensatory response in pigs.

TRIAL 1 (see Appendix 3.1)

MATERIAL AND METHODS

Twenty-three Large White x Landrace castrated male pigs of 49.2 (±1.32) kg live weight were confined in metabolism crates which allowed quantitative feeding and separate collection of faeces and urine (Figure 3.4). Four semi-synthetic diets were compounded from the ingredients detailed below in Table 3.4. The protein source was

TABLE 3.4: Chemical composition (g kg^{-1} dry matter) of dietary ingredients

Ingredient	Dry matter (g kg^{-1})	Gross energy MJ	Nitrogen	Fat	Fibre	Ash
Dried microbial cells†	893	22.6	122.55	86.0	16.4	88.19
Maize starch	864	17.1	0.50	0.8	5.6	1.52
Sucrose	999	16.4	0.17	2.0	4.0	0.36
Glucose	911	15.5	0.17	2.4	2.8	0.64
Cellulose ††	936	17.2	0.21	0.0	35.2	4.24
Maize oil	-	39.7	0.00	99.9	0.0	0.00
Mineral & vitamin mix†††	910	-	1.82	3.6	4.8	895.55

† 'Pruteen', ICI Ltd (Agricultural Division), Billingham, Cleveland.
†† 'Solka-floc', Johnson, Jorgenson and Wettre Ltd, London EC4M 7HA.
††† '1065C', Vitriton Ltd, Stamford, Lincs. PE9 2RA

dried microbial cells, 'Pruteen', which is the flash-dried product of the culture of *Methylophilus methylotrophus* on methanol. Nucleic acid-nitrogen comprised 0.188 of the total dried microbial cell nitrogen (D'Mello, Peers and Whittemore, 1976; ICI Ltd, 1976).

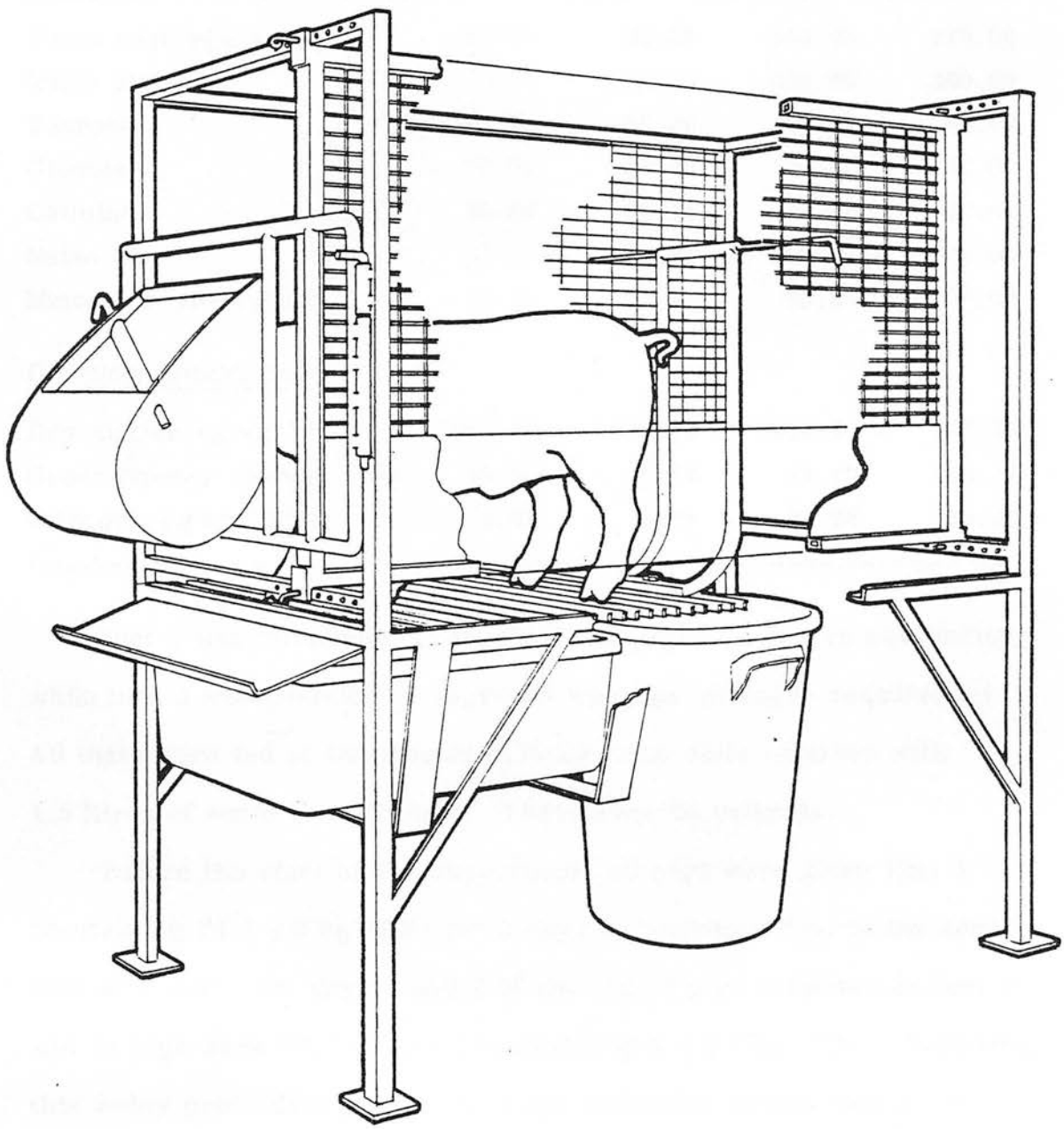


FIGURE 3.4: Metabolism crates used in nitrogen balance studies with growing pigs.

Ingredients were mixed in the proportions indicated in Table 3.5 to give four diets of differing nitrogen content.

TABLE 3.5: Ingredient and chemical composition of experimental diets

Ingredients ($g\ kg^{-1}$ fresh weight)	Diet number: 1	2	3	4
Dried microbial cells	24.75	95.50	185.00	370.00
Maize starch	725.25	657.50	565.00	380.00
Sucrose	50.00	50.00	50.00	50.00
Glucose	50.00	50.00	50.00	50.00
Cellulose	30.00	30.00	30.00	30.00
Maize oil	50.00	50.00	50.00	50.00
Mineral & vitamin mix	70.00	70.00	70.00	70.00
Chemical composition				
Dry matter ($g\ kg^{-1}$)	904.30	902.20	910.70	917.50
Gross energy ($MJkg^{-1}DM$)	16.22	17.14	17.49	18.77
Nitrogen ($g\ kg^{-1}DM$)	3.92	14.78	24.28	49.98

Diet 1 was formulated to maintain the pigs in nitrogen equilibrium, while Diet 3 was intended to approach the pigs' nitrogen requirement. All diets were fed at the rate of 0.75 kg twice daily together with 1.5 litres of water at each feed. There were no refusals.

Before the start of the experiment, all pigs were given Diet 3 (containing 24.3 $g\ N\ kg^{-1}DM$) for 3 days to accustom them to the semi-synthetic diet. On days 1 and 2 of the trial 6 pigs remained on Diet 3 and 17 pigs were offered Diet 1 (containing 3.9 $g\ N\ kg^{-1}DM$). Following this 2-day prefeeding period, a 10-day collection period took place between days 3 and 12 (balance period 1) (see Table 3.6 for the experimental design). Subsequent to day 12, 6 pigs remained on Diet 3

TABLE 3.6: Design of experiment to determine the effect of feeding diets of differing nitrogen content to pigs after a period of nitrogen deprivation

No. of pigs	Balance period: 1	2	3	4	5
	Length of balance period (days):[5] 10	5	5	5	5
6	*1*-1[1]	1-*1*	1-*1*	-	-
5	*3*-3[3]	3-*3*	3-*3*	-	-
4	*1*-2[2]	1-*2*	1-*2*	-	-
4	*1*-3	1-*3*	1-*3*	1-3-*3*[6]	1-3-*3*[6]
4	*1*-4[4]	1-*4*	1-*4*	1-4-*4*[6]	1-4-*4*[6]

[1]Diet 1 contained 3.92 gN and 16.22 MJGE kg^{-1}DM
[2]Diet 2 contained 14.78 gN and 17.14 MJGE kg^{-1}DM
[3]Diet 3 contained 24.28 gN and 17.49 MJGE kg^{-1}DM
[4]Diet 4 contained 49.49 gN and 18.77 MJGE kg^{-1}DM
[5]Prefeeding period prior to balance period 1 lasted for 2 days. 48 hours without excreta collection separated balance periods 1 and 2.
[6]2 pigs per treatment only in balance periods 4 and 5.

(treatment 3-*3*), 5 pigs remained on Diet 1 (treatment 1-*1*) and 4 pigs were allocated to Diet 2 (containing 14.8 gN kg^{-1} DM, treatment 1-*2*), 4 to Diet 3 (treatment 1-*3*) and 4 to Diet 4 (containing 50 gN kg^{-1} DM, treatment 1-*4*). Days 13 and 14 were further preliminary feeding days and no collection of excreta took place. Between days 15 and 19 and days 20 and 24, two 5-day balances were carried out, balance periods 2 and 3 respectively. Four pigs were continued on balance for an additional two 5-day periods: treatments 1-*3* and 1-*4* (2 pigs on each), 25 to 29 days, balance period 4 and 30 to 34 days, balance period 5.

Bulk 5- or 10-day collections of excreta were preserved at pH 3-3.5 by the addition of dilute sulphuric acid. Samples were

chemically analysed for nitrogen by Kjeldahl digestion and for gross energy by adiabatic bomb calorimetry.

Digestibility coefficients and daily nitrogen retentions were compared by analysis of variance.

RESULTS

Daily intakes of dry matter, gross energy and nitrogen are presented in Table 3.7 below.

TABLE 3.7: Daily intakes of dry matter (DM), gross energy (GE) and nitrogen (N) by pigs given experimental diets of differing nitrogen content

	Diet number:			
	1	2	3	4
Fresh weight (kg day^{-1})	1.500	1.500	1.500	1.500
DM (kg day^{-1})	1.356	1.353	1.366	1.376
GE (MJ day^{-1})	21.98	23.19	23.90	25.84
N (g day^{-1})	5.31	20.00	33.17	67.41

Daily nitrogen losses from pigs given Diet 1 (treatment 1-1; 17 pigs in balance period 1, 5 pigs in balance periods 2 and 3) were considered as estimates of metabolic faecal nitrogen (MFN) and endogenous urinary nitrogen (EUN); the values obtained are given in Table 3.8.

The significant difference in MFN between balance period 1 and balance periods 2 and 3 may be attributable to "carry-over" effects from the three days prior to the start of the experiment when Diet 3 was offered. A preliminary feeding period of 2 days on Diet 1 may have been insufficient to alter the nitrogen excretion rate in the faeces from one commensurate with Diet 3 to one appropriate to Diet 1. However, for the purpose of calculating true digestibility of nitrogen and the

TABLE 3.8: Metabolic faecal nitrogen (MFN) and endogenous urinary nitrogen (EUN) losses (g day^{-1}) in balance periods 1, 2 and 3 for pigs on dietary treatment 1-1 (Diet 1 contained 3.9 gN kg^{-1}DM)

Balance period:	1	2	3	SE of treatment means 1	SE of treatment means 2 & 3	Significance of difference between bal. periods
Number of pigs	17	5	5			
MFN	1.84	1.27	1.23	0.073	0.135	***
EUN	3.86	3.76	4.17	0.127	0.235	NS

biological value of the protein source, MFN and EUN estimates were averaged over the three balance periods to give 1.62 (±0.089) g MFN day^{-1} and 3.90 (±0.147) g EUN day^{-1}. Equivalent nitrogen losses for pigs offered Diet 3 (dietary treatment 3-3: balance period 1, 6 pigs and balance periods 2 and 3, 6 pigs) were 2.65 (±0.126) g in faeces and 15.48 (±0.972) g in urine.

Table 3.9 gives the nitrogen retentions and digestibility coefficients in balance period 1 (days 3 to 12) for pigs fed Diet 1 (5.31 gN day^{-1}) and Diet 3 (33.2 gN day^{-1}).

The nitrogen retention of pigs given Diet 1 (-0.32 g day^{-1}), although variable, suggested them to be close to nitrogen balance. Apparent digestibility of nitrogen was significantly lower on this diet due to the high loading of MFN relative to nitrogen intake. Calculation of the true digestibility of nitrogen [((N intake - (faecal N - MFN)) ÷ N intake)] revealed the nitrogen from Diets 1 and 3 to be absorbed with equal efficiency.

TABLE 3.9: Nitrogen retention and digestibility of gross energy and nitrogen in balance period 1 (days 3 to 12 of the experiment) for pigs given Diets 1 and 3 (containing 3.9 and 24.3 gN kg^{-1}DM respectively)

	Diet number: 1	Diet number: 3	Significance of difference between treatments
Number of pigs	17	5	
Nitrogen retention (g day^{-1})	-0.32 *(±0.317)*	15.06 *(±0.534)*	***
Digestibility			
gross energy (apparent)	0.95 *(±0.003)*	0.95 *(±0.005)*	NS
nitrogen (apparent)	0.65 *(±0.013)*	0.91 *(±0.022)*	***
(true)	0.96 *(±0.013)*	0.96 *(±0.022)*	NS

Nitrogen utilisation in balance periods 2 and 3 is detailed in Table 3.10; there were no significant differences between results for the two balance periods and values for the dietary treatments represent means for the period 15 to 24 days.

Apparent digestibility of gross energy was lower on treatment 1-4 than on the other three treatments ($P < 0.001$), which can be partly explained by the higher daily intake of gross energy by pigs fed Diet 4 (25.8 MJ day^{-1} vs 22.0, 23.2 and 23.9 MJ day^{-1} from Diets 1, 2 and 3). True digestibility of nitrogen was unaffected by dietary treatment ($P > 0.05$) and had a mean value over all treatments of 0.97. Pigs given the control treatment throughout the experiment (treatment 3-3, 33.2 g N day^{-1}) continued to retain 15.0 g N day^{-1} in balance periods 2 and 3, with an apparent digestibility coefficient for nitrogen of 0.93, an efficiency of nitrogen retention of 0.49 and a biological value for the dried microbial cells of 0.64.

TABLE 3.10: Nitrogen balance and digestibility coefficients for gross energy and nitrogen in balance periods 2 and 3 (15 to 24 days) for pigs given dietary treatments 3-*3*, 1-*2*, 1-*3* and 1-*4*

	Dietary treatments:				SE of treatment means:		Significance of difference between treatments
	3-*3*	1-*2*	1-*3*	1-*4*	treatment 3-3	other treatments	
N balance:							
N retention (g day^{-1})	15.04	11.19	17.77	25.86	0.996	1.220	***
N retained ÷ digested N	0.49	0.62	0.58	0.41	0.022	0.027	***
Biological value†	0.64	0.85	0.72	0.49	0.020	0.025	***
Digestibility:							
Gross energy (apparent)	0.96	0.96	0.95	0.93	0.004	0.005	***
Nitrogen (apparent)	0.93	0.90	0.93	0.95	0.006	0.007	**
(true)	0.97	0.98	0.98	0.96	0.006	0.008	NS

† $BV = \frac{\text{N intake - (faecal N-MFN) - (urinary N-EUN)}}{\text{N intake - (faecal N-MFN)}}$

Nitrogen retentions by pigs throughout the 24 days of nitrogen balance determinations are shown in Figure 3.5.

Results for treatment 3-*3* were taken as the standard against which nitrogen retentions achieved on other dietary treatments were compared. The effect of a 10-day nitrogen deprivation (Diet 1, balance period 1) was to enhance the rate of nitrogen retention in pigs given diets 2, 3 and 4 during balance periods 2 and 3. Dietary treatment 1-*3* elicited a net increase in nitrogen retention of 2.73 g N day^{-1} in balance periods 2 and 3 over and above that retained by pigs on treatment 3-*3* (15.04 vs 17.77 g N day^{-1}, $P < 0.05$). The nitrogen from treatment 1-*3* was utilised with significantly greater efficiency than the nitrogen from the control (3-*3*) treatment (0.58 vs 0.49, $P < 0.05$) and had a higher biological value (0.72 vs 0.64, $P < 0.05$). However, the highest values for efficiency of nitrogen utilisation (0.62) and biological value (0.85) were obtained on treatment 1-*2*. Pigs' responses to Diet 3 were evidence that daily nitrogen intake on Diet 2 (20.0 g day^{-1}) was below pig requirements for maximum nitrogen retention, and efficiencies for nitrogen utilisation on this diet were therefore likely to approximate to maximum values for the dried microbial cell nitrogen source. Conversely, the highest rate of nitrogen retention, achieved on treatment 1-*4* (intake 67.4 g N day^{-1}; retained 25.9 g N day^{-1}), was synonymous with the lowest efficiency of utilisation for nitrogen (0.41).

Enhanced retentions of nitrogen by realimented pigs on treatments 1-*3* and 1-*4* were still evident in balance periods 4 and 5, that is, for up to 22 days after the onset of realimentation. Average retentions over these two periods were 18.7 and 29.2 g N day^{-1} for treatments 1-*3* and 1-*4* respectively.

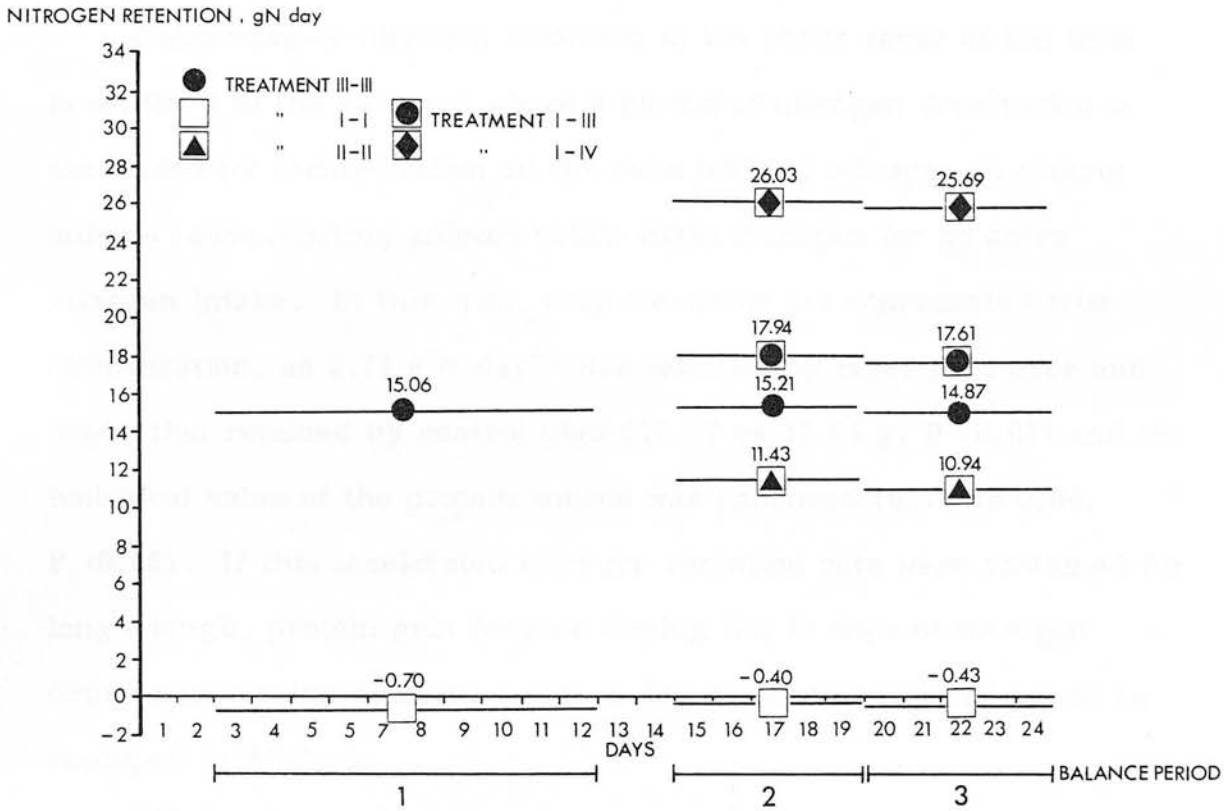


FIGURE 3.5: Nitrogen retention (g day^{-1}) in balance periods 1, 2 and 3 for pigs given dietary treatments 1-1 (□), 3-3 (•), 1-2 (▲), 1-3 (◉) and 1-4 (◆). (Diets 1, 2, 3 and 4 contained 3.9, 14.8, 24.3 and 50.0 g N kg^{-1} DM respectively.)

INTERIM DISCUSSION FOR TRIAL 1

Utilisation of the dried microbial cell protein source will be considered in the Discussion following trial 2.

Compensatory nitrogen retention in the strict sense of the term is confined to the situation where a period of nitrogen deprivation is succeeded by realimentation on the same level of nitrogen as control animals : compensating animals retain extra nitrogen for no extra nitrogen intake. In this trial, only treatment 1-3 represented true compensation, as 2.73 g N day^{-1} was retained by refed pigs over and above that retained by control pigs (17.77 vs 15.04 g, $P < 0.05$) and the biological value of the protein source was enhanced (0.72 vs 0.64, $P < 0.05$). If this accelerated nitrogen retention rate were sustained for long enough, protein gain forgone during the 12 days of nitrogen deprivation (balance period 1 plus 2-day prefeeding period) would be recouped in 67 days.

Efficiencies of nitrogen retention and biological values were significantly higher ($P < 0.001$) on treatment 1-2 than on the other three treatments, suggesting that this combination of nitrogen intakes provided the maximum possible response to the dietary protein source. Treatment 1-4 demonstrated catch-up nitrogen retention on a generous nitrogen supply, as opposed to true compensatory nitrogen retention. Pigs on treatment 1-4 retained significantly more nitrogen than 3-3 control pigs (25.86 vs 15.04 g N day^{-1}) but would not necessarily have exceeded controls' retention rate had there been a 4-4 control group. Enhanced nitrogen retention by treatments 1-3 and 1-4 in balance periods 2 and 3 were sustained for a further 10 days on the higher levels of nitrogen intake (balance periods 4 and 5).

In summary, this trial demonstrated compensatory nitrogen retention following a period of nitrogen deprivation. Refed pigs retained significantly more nitrogen per day than pigs offered the same nitrogen allowance throughout, and continued to do so for 22 days after the diet changeover was effected. Superior efficiencies of nitrogen utilisation and biological values obtained for refed pigs premisses either an ability to exploit a wider spectrum of nitrogen constituents in the protein source or an enhanced efficiency of utilisation of the usual range of nitrogen-containing components absorbed from the protein source. However, this trial did not discriminate between compensatory nitrogen retention and catch-up nitrogen retention on a more generous nitrogen allowance, nor did experimental procedures permit evaluation of the immediate consequences for nitrogen retention of changing from low- to high-nitrogen intakes, or indeed, from high- to low-nitrogen intakes.

To confirm the findings of this initial experiment, and to counter its deficiencies, a second trial was undertaken. The latter employed a control treatment for each of four diets of differing nitrogen content to facilitate comparison of nitrogen retentions of control and realimented pigs fed the same daily nitrogen allowance. All pigs were given a longer pre-feeding period prior to the first collection period, ensuring that faecal material collected was representative of current nitrogen intake. Short-term fluctuations in nitrogen excretion following a change in nitrogen intake were monitored by sub-dividing 10-day balances subsequent to the first balance period into 3-day and 7-day collection periods. In addition, dietary nitrogen intake permutations were such that it was possible to examine nitrogen excretion and retention rates produced by an abrupt reduction in nitrogen intake.

TRIAL 2

MATERIAL AND METHODS

Forty-eight Large White castrated male pigs were confined in metabolism crates which allowed quantitative feeding and separate collection of faeces and urine. There were 4 replicates with one pig per treatment in each. Initial live weights were 54.3 (±0.84), 61.0 (±0.93), 47.8 (±1.29) and 41.9 (±1.02) kg for replicates 1, 2, 3 and 4 respectively. Four semi-synthetic diets were compounded from the ingredients used in the previous experiment (Table 3.4). These ingredients were mixed in the proportions indicated in Table 3.11 to give diets of different nitrogen content.

TABLE 3.11: Ingredient and chemical composition of experimental diets

Ingredients ($g\ kg^{-1}$ fresh weight)	Diet number: 1	2	3	4
Dried microbial cells ('Pruteen')	27	150	350	450
Maize starch	723	600	400	300
Sucrose	50	50	50	50
Glucose	50	50	50	50
Cellulose	30	30	30	30
Maize oil	50	50	50	50
Mineral and vitamin mix	70	70	70	70
Chemical composition				
Dry matter ($g\ kg^{-1}$)	870.9	871.4	872.0	872.6
Gross energy ($MJ\ kg^{-1}DM$)	16.66	17.88	18.57	19.30
Nitrogen ($g\ kg^{-1}DM$)	4.47	20.35	39.49	61.15

All pigs were offered Diet 2 (containing 20.4 g N $kg^{-1}DM$) for 3 days to accustom them to the semi-synthetic diet. There followed a 7-day prefeeding period during which pigs were given the diets they

were to receive in balance period 1 (see Table 3.12 for the experimental design). All diets were fed at the rate of 0.875 kg twice daily together with 1.75 litres of water at each feed. Refusals were collected for each balance period, weighed and oven-dried. Pigs were weighed immediately preceding balance period 1. During the 10 days of this first balance period (days 1 to 11), 6 pigs from each replicate (24 pigs in total) were offered Diet 1 (containing 4.5 g N kg^{-1} DM): treatments *1*-1-1, *1*-2-2, *1*-2-2, *1*-3-3, *1*-3-1 and *1*-4-4. A further 3 pigs from each replicate were offered Diet 2: treatments *2*-2-2, *2*-1-2 and *2*-3-3. Two pigs per replicate were given Diet 3 (containing 39.5 g N kg^{-1}DM): treatments *3*-3-3 and *3*-1-3; one pig per replicate was given Diet 4 (containing 61.1 g N kg^{-1}DM): treatment *4*-4-4. On day 12 of the experiment, balance period 2 began and continued for 10 days until day 22. During this collection period, 3 pigs from each replicate were given Diet 1 (treatments 1-*1*-1, 2-*1*-2 and 3-*1*-3), 3 pigs per replicate were given Diet 2 (treatments 2-*2*-2, 1-*2*-2 and 1-*2*-1), 4 pigs per replicate were offered Diet 3 (treatments 3-*3*-3, 1-*3*-3, 1-*3*-1 and 2-*3*-3) and 2 pigs per replicate were given Diet 4 (treatments 4-*4*-4 and 1-*4*-4). Balance period 3 ran from day 23 until day 33 and for some pigs involved a second change of diet. Three pigs per replicate received Diet 1 (treatments 1-1-*1*, 1-2-*1* and 1-3-*1*), 3 pigs per replicate received Diet 2 (treatments 2-2-*2*, 1-2-*2* and 2-2-*2*), 4 pigs per replicate were given Diet 3 (treatments 3-3-*3*, 1-3-*3*, 3-1-*3* and 2-3-*3*) and 2 pigs per replicate continued to receive Diet 4 (treatments 4-4-*4* and 1-4-*4*). At the end of balance period 3 pigs were removed from the metabolism crates and reweighed.

Balance periods 2 and 3 were sub-divided into 3-day and 7-day collection periods (designated 2A, 2B, 3A and 3B in Table 3.11) to

TABLE 3.12: Experimental design to determine the effect of feeding diets of differing nitrogen content

	Balance period:					
	1	2		3		
		2A	2B	3A	3B	
Length of balance period (days)[5]:	10	3	7	3	7	
control pigs[6]	*1*-1-1[1]	1-*1*-1		1-1-*1*		
	2-2-2[2]	2-*2*-2		2-2-*2*		
	3-3-3[3]	3-*3*-3		3-3-*3*		
	4-4-4[4]	4-*4*-4		4-4-*4*		
treatment pigs[6]	*1*-2-2	1-*2*-2		1-2-*2*		
	1-2-1	1-*2*-1		1-2-*1*		
	1-3-3	1-*3*-3		1-3-*3*		
	1-3-1	1-*3*-1		1-3-*1*		
	1-4-4	1-*4*-4		1-4-*4*		
	2-1-2	2-*1*-2		2-1-*2*		
	3-1-3	3-*1*-3		3-1-*3*		
	2-3-3	2-*3*-3		2-3-*3*		

[1] Diet 1 contained 4.47 g N and 16.66 MJGE kg^{-1}DM

[2] Diet 2 contained 20.35 g N and 17.88 MJGE kg^{-1}DM

[3] Diet 3 contained 39.49 g N and 18.57 MJGE kg^{-1}DM

[4] Diet 4 contained 61.15 g N and 19.30 MJGE kg^{-1}DM

[5] Prefeeding period prior to balance period 1 lasted for 7 days. 24 hours without excreta collection separated balance periods 1 and 2A and 2B and 3A

[6] 4 pigs per dietary treatment

monitor the short-term (3-day) and longer-term (7-day) responses to alterations in dietary nitrogen level. When diets were changed between balance periods 1 and 2, and again between balance periods 2 and 3, no excreta was collected for 24 hours (days 11 to 12, 22 to 23) in order to ensure that faecal material sampled from periods 2A and 3A was representative of newly-introduced diets.

Bulk collections of faeces and urine were preserved at pH 4.5-5.5 and 2-3 by addition of dilute sulphuric acid. The pH standard for faeces was a compromise between the recommended pH for minimisation of ammonia loss to the atmosphere (pH 5-6) and a pH which, if exceeded, would permit microbial growth (pH >4) (Crooks, personal communication). Feed and faecal samples for chemical analysis were oven-dried to constant weight at 95°C and then milled. Urine sub-samples were strained through muslin to remove hair, skin and other debris. Chemical analysis was for nitrogen by Kjeldahl digestion and for gross energy by adiabatic bomb calorimetry. Feed and faeces samples were also analysed for ash, fat and TCA fibre in replicates 3 and 4.

Digestibility coefficients and nitrogen balances were compared by analysis of variance using the Genstat 4.01 statistical package (Lawes Agricultural Trust, 1977). There were significant differences between replicates for these parameters so that the interaction between diet and replicate was tested wherever pig numbers and residual variation permitted.

RESULTS

Daily intakes of dry matter, gross energy and nitrogen are presented in Table 3.13.

TABLE 3.13: Daily intakes of dry matter (DM), gross energy (GE) and nitrogen (N) by pigs given experimental diets of differing nitrogen content

	Diet number: 1	2	3	4
Fresh weight (kg)	1.750	1.750	1.750	1.750
DM (kg)†	1.524	1.525	1.526	1.527
GE (MJ)	25.57	27.27	28.34	29.48
N (g)	6.90	31.03	60.42	93.37

†Replicate 1 - no refusals

Replicate 2 - balance period 3B: treatment 1-1-*1* ate 1.415 kg DM day^{-1}
treatment 1-3-*1* ate 1.306 kg DM day^{-1}

Replicate 3 - balance period 1: treatment *1*-1-1 ate 1.484 kg DM day^{-1}, pig was then removed from subsequent balance periods due to inappetence and chronic bloat

Replicate 4 - balance period 1: treatment *1*-1-1 ate 1.376 kg DM day^{-1}
treatment *1*-2-2 ate 1.410 kg DM day^{-1}

It was noticeable that all refusals arose in pigs offered Diet 1, which suggests considerably reduced palatability for very low protein diets (0.028 CP in the dry matter).

Daily nitrogen losses by pigs given Diet 1 (balance period 1, 24 pigs; balance periods 2B and 3B, treatment 1-1-1, 6 pigs) were used as estimates of metabolic faecal nitrogen (MFN) and endogenous urinary nitrogen (EUN) and appear in Table 3.14 overleaf.

Mean daily nitrogen losses by pigs on Diet 1 were 3.96 g EUN (n=30) and 1.92 g MFN (n=30). There were no significant differences in MFN between replicates or between balance periods. EUN was

TABLE 3.14: Metabolic faecal nitrogen (MFN) and endogenous urinary nitrogen (EUN) losses (g day^{-1}) in balance period 1 for pigs offered Diet 1 and in balance periods 2B and 3B for pigs on treatment 1-1-1. (Diet 1 contained 4.5 g N kg^{-1}DM.)

Balance period:	1	2B	3B	SE of treatment means 1	SE of treatment means 2B & 3B	Significance of difference between treatment means
Number of pigs	24	3	3			
MFN	1.90	2.01	2.01	0.113	0.321	NS
EUN	3.98	3.97	3.79	0.280	0.480	NS

similarly unaffected by time on balance, but there were distinct differences between replicates ($P < 0.001$): heavier pigs in replicates 1 and 2 lost a greater daily quantity of endogenous urinary nitrogen (4.95 ± 0.242 g day^{-1}, n=16) than the lighter pigs in replicates 3 and 4 (2.83 ± 0.115 g day^{-1}, n=14).

Control pigs, balance periods 1, 2 and 3

Nitrogen balance and digestibility coefficients for control pigs (treatments 1-1-1, 2-2-2, 3-3-3 and 4-4-4) in balance periods 1, 2A, 2B, 3A and 3B are given in Table 3.15. Mean daily nitrogen retentions over the 30 days of excreta collection were 0.57 (±0.288), 17.37 (±0.979), 22.01 (±0.894) and 31.93 (±2.008) g for diets 1 to 4 respectively. Daily nitrogen retentions by control pigs are presented in Figure 3.6. Average biological values for diets 1 to 4 were 0.98 (±0.047), 0.77 (±0.026), 0.48 (±0.017) and 0.42 (±0.021). Efficiency of nitrogen utilisation, calculated as the proportion of nitrogen digested which was retained per day, was highest on Diet 2 at 0.56; Diet 1 was used with lowest efficiency, while Diets 3 and 4 were intermediate.

TABLE 3.15: Nitrogen balance and digestibility coefficients for gross energy and nitrogen for pigs fed diets 1, 2, 3 and 4 (containing 4.5, 20.4, 39.5 and 61.1 g N kg^{-1} DM respectively) in balance periods 1, 2A, 2B, 3A and 3B

	Diet No. 1					Diet No. 2					Diet No. 3					Diet No. 4					SE of difference between	
Balance period:	1	2A	2B	3A	3B	1	2A	2B	3A	3B	1	2A	2B	3A	3B	1	2A	2B	3A	3B	(i) diet means	(ii) balance periods within diets
Length of balance period (days)	10	3	7	3	7	10	3	7	3	7	10	3	7	3	7	10	3	7	3	7		
No. of pigs	4	3	3	3	3	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4		
Nitrogen retention (g day^{-1})	0.77	0.98	0.74	-0.45	0.75	16.20	19.47	16.62	17.43	17.65	23.08	23.93	23.20	19.63	20.08	32.36	33.34	33.42	30.50	30.05	1.151***	2.573 NS
Nitrogen retained (g day^{-1}) ÷ nitrogen digested (g day^{-1})	0.15	0.19	0.16	-0.16	0.18	0.57	0.66	0.59	0.64	0.62	0.41	0.41	0.42	0.34	0.36	0.37	0.38	0.38	0.35	0.34	0.044***	0.097 * diet 1 only others NS
Biological value	1.00	1.00	1.02	0.83	1.05	0.73	0.81	0.75	0.80	0.78	0.50	0.50	0.51	0.43	0.44	0.43	0.43	0.44	0.41	0.40	0.028***	0.062 * diet 1 only others NS
Digestibility coefficients:																						
gross energy (apparent)	0.95	0.97	0.95	0.95	0.94	0.95	0.97	0.94	0.93	0.95	0.94	0.96	0.93	0.95	0.94	0.92	0.92	0.92	0.92	0.91	0.005*** diet 4 only others NS	0.012 NS
nitrogen (apparent)	0.73	0.80	0.70	0.67	0.69	0.91	0.94	0.90	0.89	0.91	0.93	0.96	0.93	0.94	0.94	0.93	0.94	0.94	0.93	0.93	0.011***	0.025 **diet 1 only others NS
nitrogen (true)	1.02	1.11	0.99	0.95	0.99	0.97	1.00	0.96	0.95	0.97	0.96	0.99	0.96	0.97	0.97	0.95	0.96	0.96	0.95	0.95	0.010***	0.022 **diets 1 & 2 only others NS

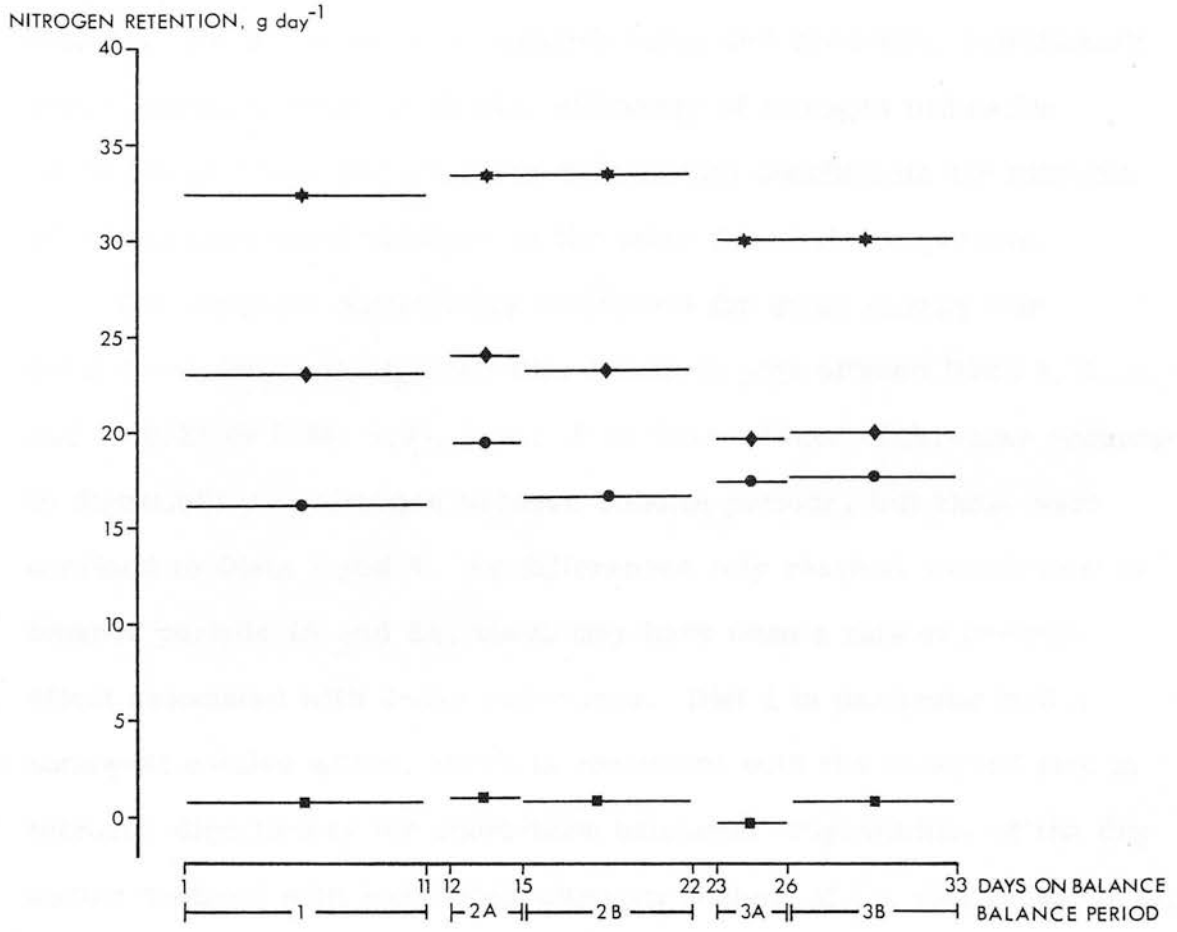


FIGURE 3.6: Daily nitrogen retention in balance periods 1, 2A, 2B, 3A and 3B by control pigs given diets 1 (■), 2 (●), 3 (♦) and 4 (✱). (Diets 1 to 4 contained 4.5, 20.4, 39.5 and 61.1 g N kg^{-1} DM respectively.)

One pig fed Diet 1 was in negative nitrogen balance to the order of -2 g day^{-1} during balance period 3A, reducing the average nitrogen retention for the group to a negative value and producing significantly lower biological value ($P < 0.05$), efficiency of nitrogen utilisation ($P < 0.05$) and true and apparent digestibility coefficients for nitrogen ($P < 0.01$) than those obtained in the other four balance periods.

The apparent digestibility coefficient for gross energy was consistently lower in pigs fed Diet 4 than in pigs offered Diets 1, 2 and 3 (0.92 vs 0.95, 0.95, 0.94; $P < 0.001$). Minor differences occurred in digestibility of nitrogen between balance periods, but these were confined to Diets 1 and 2. As differences only reached significance in balance periods 2A and 3A, there may have been a rate of passage effect associated with 3-day collections. Diet 1 in particular had a somewhat costive action, which is consistent with the observed rise in nitrogen digestibility for short-term balances. Digestibility of the dry matter declined with increasing nitrogen content of the diet (0.93, 0.93, 0.91 and 0.89 for Diets 1 to 4 respectively, s.e.d. 0.004, $P < 0.001$). Apparent digestibility of fibre (replicates 3 and 4 only) was lower on Diet 4 than the other three diets (0.45 vs 0.62, $P < 0.01$), augmenting a subjective assessment of more rapid rate of transit for pigs offered this diet. The digestibility coefficient for fat was very much lower with Diet 1 (0.49 vs 0.84, $P < 0.001$) than with Diets 2, 3 and 4.

Treatment pigs, differences between 3-day and 7-day balance periods

All treatment pigs received a change in dietary nitrogen intake at the end of balance period 1. Full results of nitrogen balance and digestibility coefficients in balance periods 2A and 2B and 3A and 3B are given in Appendices 3.2 to 3.4. Daily nitrogen retentions in these four balance periods are presented in Figures 3.7 to 3.10.

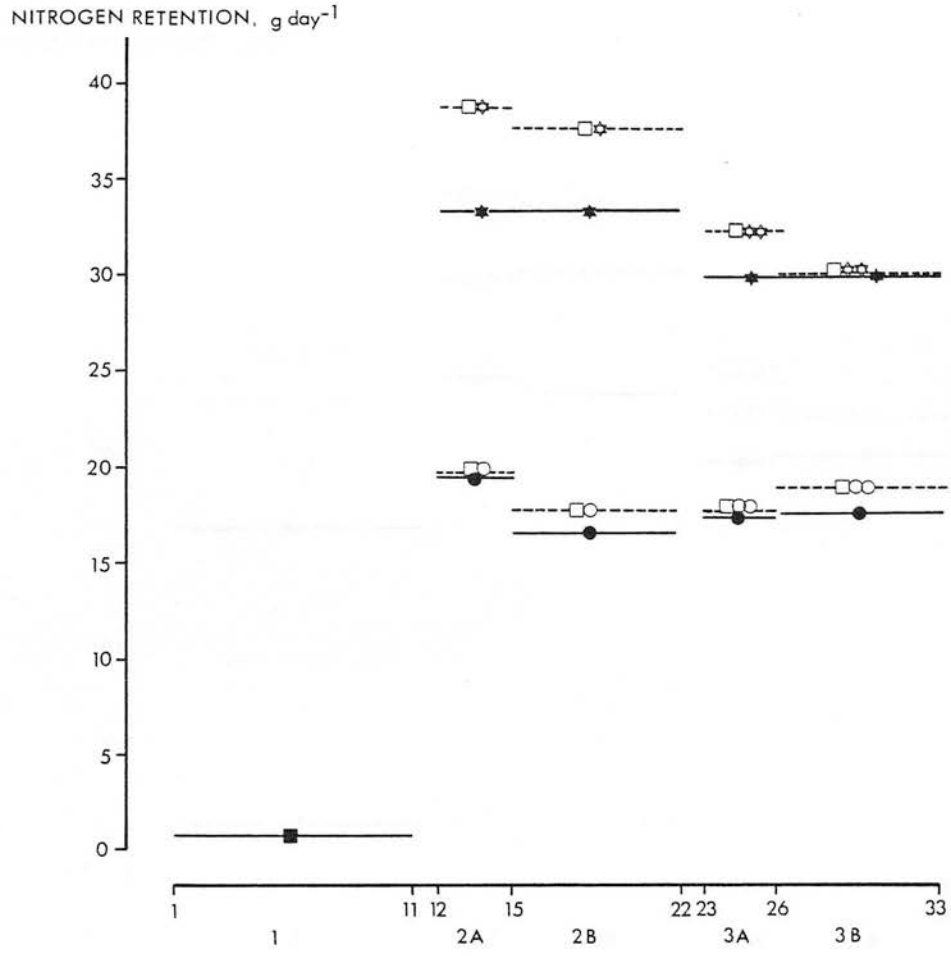


FIGURE 3.7: Daily nitrogen retention in balance periods 2A, 2B, 3A and 3B by pigs given diet 1 in balance period 1 and realimented on diets 2 and 4 in balance periods 2 and 3: treatments 1-2-2 (□○,□○○) and 1-4-4 (□✧,□✧✧).

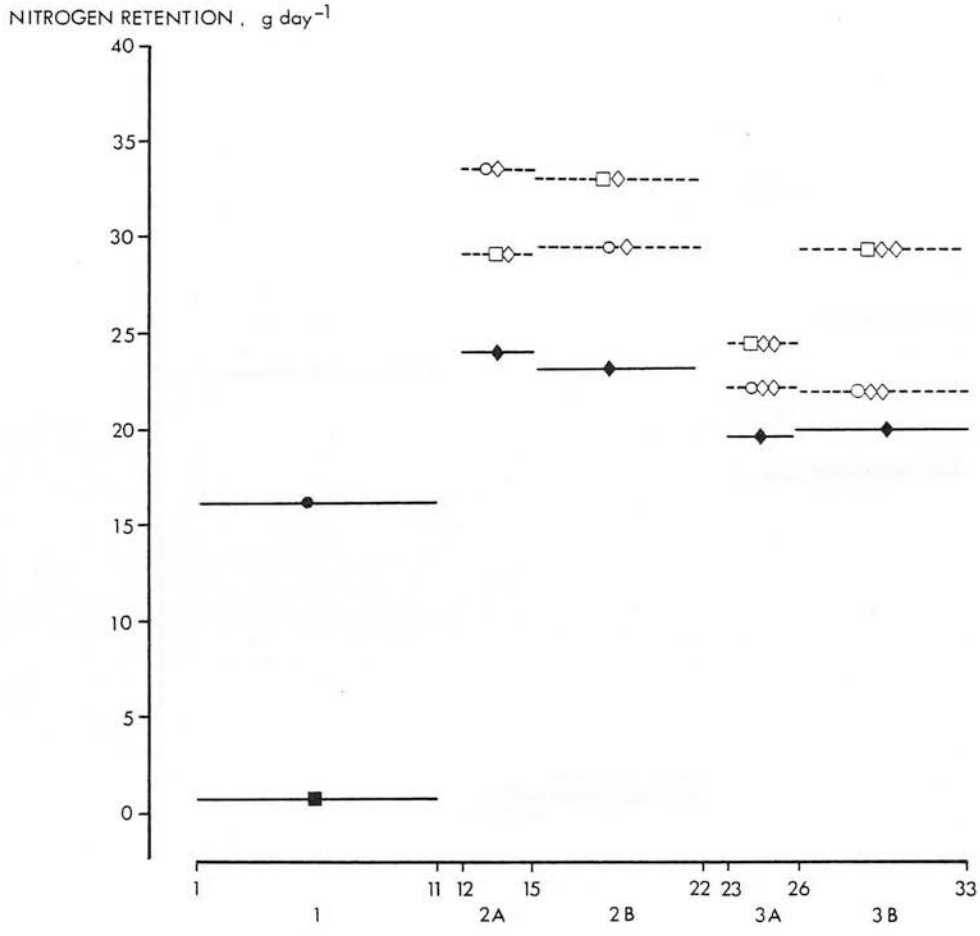


FIGURE 3.8: Daily nitrogen retention in balance periods 2A, 2B, 3A and 3B by pigs given diets 1 and 2 in balance period 1 and realimented on diet 3 in balance periods 2 and 3: treatments 1-3-3 (□◊, □◊◊) and 2-3-3 (○◊, ○◊◊).

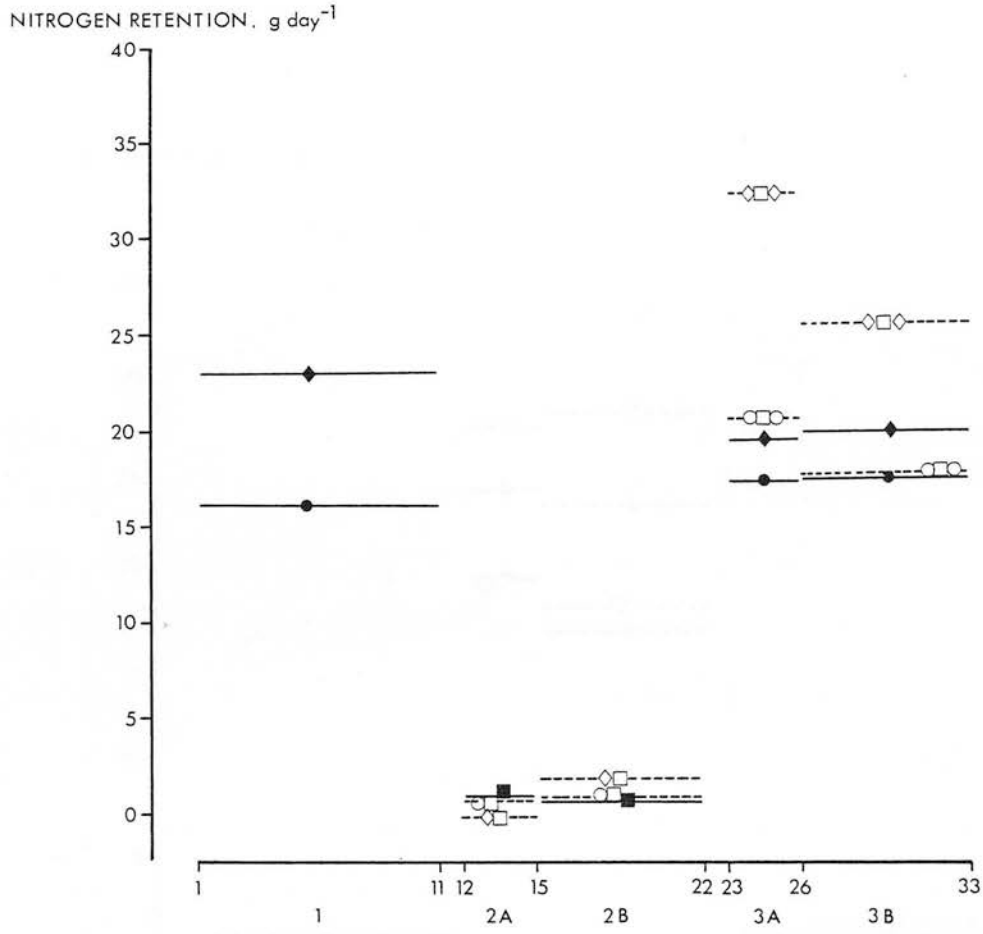


FIGURE 3.9: Daily nitrogen retention in balance periods 2A, 2B, 3A and 3B by pigs given diets 2 and 3 in balance period 1, diet 1 in balance period 2 and realimented on diets 2 and 3 in balance period 3: treatments 2-1-2 (○□,○□○) and 3-1-3 (◊○,◊○◊).

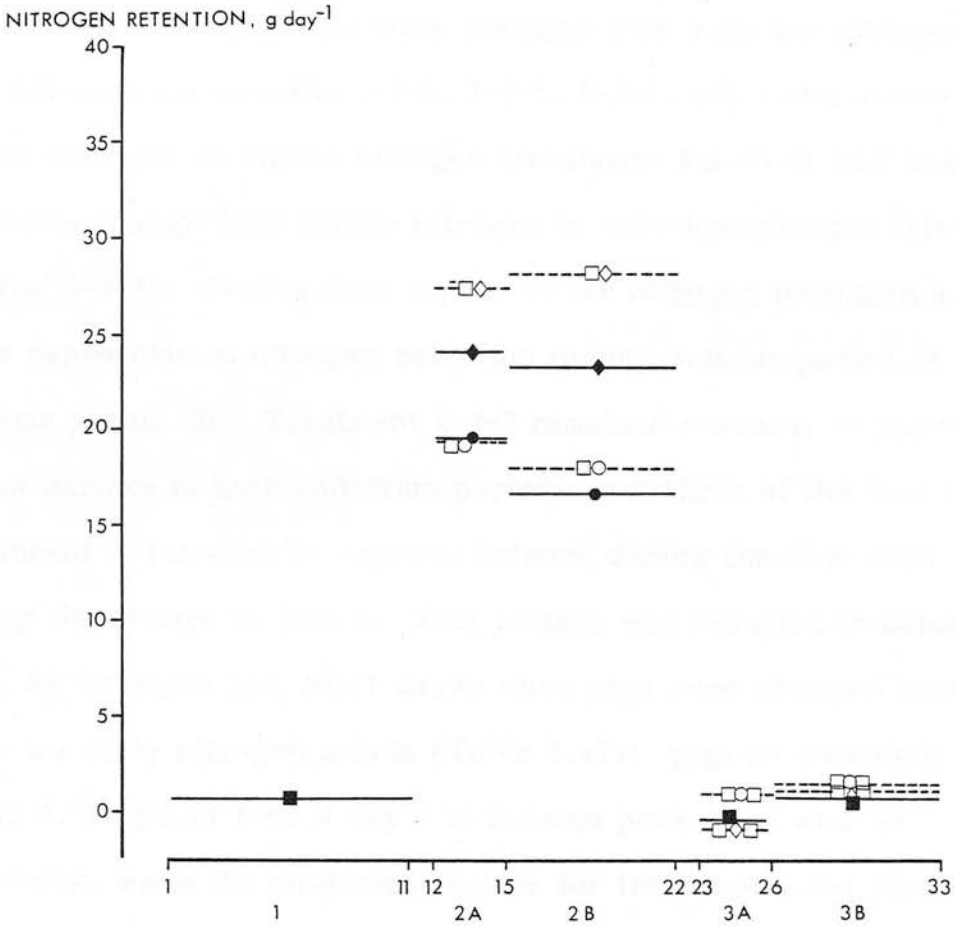


FIGURE 3.10: Daily nitrogen retention in balance periods 2A, 2B, 3A and 3B by pigs given diet 1 in balance period 1, realimented on diets 2 and 3 in balance period 2 and returned to diet 1 in balance period 3: treatments 1-2-1 (□○,□○□) and 1-3-1 (□◇,□◇□).

Nitrogen balance in balance periods 2A (3 days) and 2B (7 days) for pigs given a change in dietary nitrogen intake at the end of balance period 1 is shown in Table 3.16. The nitrogen retentions were not significantly different for three-day collections as opposed to seven-day collections, whether pigs had been changed from very low nitrogen to higher nitrogen (treatments 1-*2*-2, 1-*2*-1, 1-*3*-3, 1-*3*-1 and 1-*4*-4), from moderate nitrogen to higher nitrogen (treatment 2-*3*-3) or had undergone the reverse change from higher nitrogen to very low nitrogen (treatments 2-*1*-2 and 3-*1*-3). Moving from higher to low nitrogen produced a greater depression in nitrogen retention during balance period 2A than in balance period 2B. Treatment 2-*1*-2 remained narrowly in positive nitrogen balance in both collection periods, but three of the four pigs on treatment 3-*1*-3 were in negative balance during the four days following the change to Diet 1. This pattern was repeated in balance periods 3A (3 days) and 3B (7 days) when pigs were changed from higher to very low daily nitrogen intake (Table 3.17); pigs on treatment 1-2-*1* retained 0.78 g and 1.42 N day^{-1} in balance periods 3A and 3B respectively, while the equivalent values for treatment 1-3-*1* were -0.85 and 1.17 g N day^{-1}.

Contrary to the similarity in nitrogen balance between balance periods 2A and 2B for pigs given higher intakes of nitrogen after 17 days on low nitrogen intake, the same sequence of nitrogen intakes in balance periods 3A and 3B caused an elevation in nitrogen retained in 3A relative to that in 3B. This reached significance for pigs rehabilitated on Diet 3: treatment 3-1-*3* engendered the retention of an extra 6.8 g N day^{-1} in balance period 3A ($P < 0.05$), thus raising the biological value for the nitrogen source to 0.65. During balance period 3B, the biological value obtained on this treatment was reduced to 0.55.

TABLE 3.16: Nitrogen balance in balance periods 2A (3 days) and 2B (7 days) for pigs given a change in dietary nitrogen intake from the end of balance period 1

	Diet No.: 1		2		3		4				SE of difference between balance periods 2A & 2B
	2-*1*-2	3-*1*-3	1-*2*-2	1-*2*-1	1-*3*-3	1-*3*-1	2-*3*-3		1-*4*-4		
Balance period	2A	2B	2A	2B	2A	2B	2A	2B	2A	2B	
No. of pigs	8	8	8	8	7	8	4	4	4	4	
Nitrogen retention (g day^{-1})	0.37	1.37	19.48	17.86	28.10	30.25	33.60	29.52	39.08	37.72	1.980[1] 1.715[2] NS 1.400[3]
Nitrogen retained ÷ nitrogen digested	0.07	0.24	0.67	0.63	0.48	0.53	0.59	0.52	0.44	0.42	0.036 0.031 NS 0.025
Biological value	0.94	1.05	0.82	0.78	0.57	0.62	0.67	0.61	0.50	0.48	0.035 0.030 NS 0.025

[1] n per treatment = 4
[2] n = 4 vs 8
[3] n per treatment = 8

TABLE 3.17: Nitrogen balance in balance periods 3A (3 days) and 3B (7 days) for pigs given a change in dietary nitrogen intake from the end of balance period 2B

	Diet No. 1		SE of difference between balance periods 3A & 3B	*Diet No.* 2		*Diet No.* 3		SE of difference between balance periods 3A & 3B
	1-2-*1*	1-2-*1*		2-1-*2*		3-1-*3*		
Balance period	3A	3B		3A	3B	3A	3B	
No. of pigs	8	8		4	4	4	4	
Nitrogen retention (g day^{-1})	0.24	1.29	1.112 NS	20.71	17.77	32.45	25.64	1.892* Diet 3 only
Nitrogen retained ÷ nitrogen digested	0.04	0.25	0.337 NS	0.70	0.65	0.57	0.46	0.034* Diet 3 only
Biological value	0.93	1.05	0.160 NS	0.85	0.81	0.65	0.55	0.034* Diet 3 only

There were no differences in nitrogen balance for pigs remaining on the same diet in balance period 3 as they had received during balance period 2 (treatments 1-2-*2*, 2-3-*3* and 1-4-*4*), with the exception of treatment 1-3-*3* in which retention in balance period 3A exceeded retention in balance period 3B by 4.9 g N daily ($P < 0.05$).

Comparison between control and treatment pigs, balance period 2B

Owing to the inherently greater variation associated with nitrogen balances carried out over less than 5 or 6 days (Thorbek, 1975), it was decided to confine comparison of results for control and treatment pigs to the 7-day balance periods (2B and 3B).

Table 3.18 details the nitrogen balance in balance period 2B for pigs given a change in dietary nitrogen intake at the end of balance period 1. As in the case of control pigs, daily nitrogen retentions followed the pattern of dietary nitrogen intake with mean daily nitrogen retentions for Diets 1 to 4 of 1.37 (±0.448), 17.86 (±0.890), 29.98 (±1.219) and 37.72 (±3.932) g. All treatment pigs were found to retain more nitrogen daily than their respective control pigs but because of variation between the four replicates (which accounted for 0.12 of total variation in this analysis), only the most pronounced of the elevations in nitrogen retentions reached significance. Pigs on treatments 1-*3*-3, 1-*3*-1 and 2-*3*-3 retained, on average, 7.04 g N day^{-1} in balance period 2B in excess of the 23.2 g N day^{-1} retained by 3-3-*3* control pigs. Treatments 1-*2*-2 and 1-*2*-1 produced the smaller (and non-significant) advantage of 1.24 g N day^{-1} over 2-*2*-2 controls, while treatment 1-*4*-4 pigs retained 4.29 g N day^{-1} more than pigs fed Diet 4 throughout, but this difference also failed to reach significance.

Increases in nitrogen retention by rehabilitated pigs in balance period 2B led to higher efficiencies of nitrogen utilisation and biological

TABLE 3.18: Nitrogen balance period 2B (7 days) for pigs given a change in dietary nitrogen intake from the end of balance period 1

	Diet No.: 1			2			3				4		SE of difference between treatments within diets	
	1-1-1	2-1-2	3-1-3	2-2-2	1-2-2	1-2-1	3-3-3	1-3-3	1-3-1	2-3-3	4-4-4	1-4-4		
No. of pigs	3	4	4	4	4	4	4	4	4	4	4	4		
Nitrogen retention (g day^{-1})	0.74	0.89	1.84	16.62	17.76	17.96	23.20	33.05	28.15	29.52	33.43	37.72	3.911*	diet 3 only rest NS
Nitrogen retained ÷ nitrogen digested	0.16	0.14	0.34	0.59	0.62	0.63	0.42	0.58	0.50	0.52	0.38	0.42	0.102	NS
Biological value	1.02	1.03	1.06	0.75	0.78	0.78	0.51	0.66	0.58	0.61	0.44	0.48	0.088	NS

value than equivalent values for control pigs, although none of these increases achieved significance.

Consistent with digestibility coefficients for control pigs, animals realimented on Diet 4 had lower apparent digestibility of gross energy than pigs realimented on Diets 2 and 3 ($P < 0.01$). As expected, apparent digestibility of nitrogen was lowest for pigs offered Diet 1 ($P < 0.05$) due to the higher loading of metabolic nitrogen loss on this low nitrogen diet. Digestibility coefficients did not differ between control and realimented pigs on the same diet.

Comparison between control and treatment pigs, balance period 3B

Nitrogen balances in balance period 3B for pigs given a change in dietary nitrogen intake at the end of balance period 2B and for pigs given the same dietary nitrogen intake as in balance periods 2A and 2B are given in Table 3.19.

Pigs continued on Diet 2 in balance period 3B (treatment 1-2-*2*) maintained exactly the same small advantage over control pigs by retaining 1.25 g extra N day^{-1}. Treatment 1-3-*3* continued to retain significantly more nitrogen than Diet 3 controls (9.34 g extra N day^{-1}, $P < 0.05$) but the other 4 pigs continued on Diet 3 (treatment 2-3-*3*) made similar retentions in balance period 3B to those of controls (21.98 vs 20.08 g N day^{-1}). Further, treatment 1-4-*4* realised daily retentions in 3B which were indistinguishable from those of 4-4-*4* controls (30.20 vs 30.05 g N day^{-1}).

Refeeding with higher nitrogen after 10 days of low nitrogen in balance period 2 did not promote a significant elevation in nitrogen retention by treatments 2-1-*2* and 3-1-*3* over their respective controls when the comparison is made for the 7-day collection of balance period 3B.

TABLE 3.19: Nitrogen balance in balance period 3B (7 days) for pigs given a change in dietary nitrogen intake from the end of balance period 2B and for pigs given the same dietary nitrogen intake as in balance periods 2A and 2B

	Diet No.: 1			2			3				4		SE of difference between treatments within diets
	1-1-*1*	1-2-*1*	1-3-*1*	2-2-*2*	1-2-*2*	2-1-*2*	3-3-*3*	1-3-*3*	2-3-*3*	3-1-*3*	4-4-*4*	1-4-*4*	
No. of pigs	*3*	4	4	*4*	4	4	*4*	3	4	4	*4*	4	
Nitrogen retention (g day^{-1})	*0.75*	1.42	1.17	*17.65*	18.90	17.77	*20.08*	29.42	21.98	25.64	*30.05*	30.20	3.102* diet 3 only
Nitrogen retained ÷ nitrogen digested	*0.18*	0.25	0.25	*0.62*	0.66	0.65	*0.36*	0.51	0.39	0.46	*0.34*	0.35	0.072 NS
Biological value	*1.05*	1.07	1.04	*0.78*	0.81	0.81	*0.44*	0.60	0.48	0.55	*0.40*	0.41	0.078 NS

Mean daily nitrogen retentions in balance period 3B by pigs fed Diets 1 to 4 were 1.29 (±0.336), 18.33 (±1.036), 25.34 (±1.357) and 30.20 (±3.272) g. Control and treatment pigs on the same diet had similar digestibility coefficients.

Daily liveweight gains (kg) by pigs in replicates 1,3 and 4 during their 32-day confinement in metabolism cages are presented in Table 3.20. Highest daily gains were made by pigs in replicate 4, the lightest pigs at the start of the experiment, and presumably, those pigs for whom the fixed feed allowance was least restrictive in the early stages of time on test.

TABLE 3.20: Daily liveweight gain (kg) by castrated male pigs retained in metabolism cages for 32 days and fed diets of differing nitrogen content

Dietary treatment	Daily liveweight gain (kg): Replicate 1	Replicate 3	Replicate 4	Mean
1-1-1	0.371	-	0.437	0.404
2-2-2	0.557	0.529	0.734	0.607
3-3-3	0.643	0.471	0.757	0.624
4-4-4	0.629	0.629	0.800	0.686
1-2-2	0.443	0.457	0.586	0.495
1-2-1	0.329	0.386	0.429	0.381
1-3-3	0.586	0.571	0.711	0.623
1-3-1	0.429	0.386	0.557	0.457
1-4-4	0.557	0.514	0.537	0.536
2-1-2	0.543	0.471	0.580	0.531
3-1-3	0.543	0.486	0.729	0.586
2-3-3	0.571	0.586	0.669	0.609
Overall mean				0.549

DISCUSSION

Utilisation of the dried microbial cell protein source in semi-synthetic diets

The use of semi-synthetic diets in Trials 1 and 2 did not preclude acceptable growth rates: control pigs on Trial 2 fed Diets 2, 3 and 4 gained an average of 0.64 kg live weight day^{-1} during their 32-day confinement in metabolism cages (weight range 45 to 70 kg). Large White pigs kept continuously in balance cages between 30 and 70 kg live weight and offered a conventional diet according to a weight scale gained 0.66 kg live weight daily (Livingston, Fuller and Livingstone, 1969).

Digestibility coefficients, biological values and efficiencies of nitrogen utilisation for the dried microbial cell protein source are summarised in Table 3.21. There was good agreement between Trials 1 and 2 and D'Mello *et al* (1976) as to the digestibility and utilisation of the dried microbial cells in diets containing comparable levels of nitrogen and gross energy. The single-cell protein assessed by Schulz and Oslage (1976) comprised a lower proportion of nitrogen in its dry matter than the "Pruteen" used in the other three trials (0.082 vs 0.122), which may account for its reduced digestibility. The advantage in biological value and efficiency of nitrogen utilisation measured by D'Mello *et al* (1976) relative to those generated in the present trials could be linked to the less generous energy allowance used in the former experiment (0.60 MJDE g^{-1} digested N vs 0.75 and 0.70 MJDE g^{-1} digested N, Trials 1 and 2 respectively).

Of the nitrogen contained in dried microbial cells, approximately 0.19 is nucleic-acid nitrogen (D'Mello *et al*, 1976). Biological values for the nitrogen source measured in pigs given Diet 1 averaged at

TABLE 3.21: Digestibility coefficients, biological value and efficiency of nitrogen utilisation for dried microbial cell protein contained in semi-synthetic diets for growing pigs

	Source:			
	Trial 1[1]	Trial 2[1]	D'Mello, Peers[1] & Whittemore (1976)	Schulz &[2] Oslage (1976)
Number of pigs	6[3]	8[4]	8[5]	-
Digestibility coefficients:				
Dry matter (apparent)	0.92	0.92	0.91	-
Gross energy (apparent)	0.96	0.94	0.95	0.80
Nitrogen (apparent)	0.92	0.92	0.94	0.84
Nitrogen (true)	0.97	0.97	0.98	-
Biological value	0.64	0.63	0.68	0.79[6]
Nitrogen retained ÷ nitrogen digested	0.49	0.50	0.55	-

[1] dried microbial cell protein, 'Pruteen' (ICI Agricultural Division, Billingham)

[2] bacterium grown on methanol

[3] diet 3 only, containing 24.3 gN and 17.5 MJ GE kg^{-1} DM

[4] diets 2 and 3 containing 20.4, 39.5 gN and 17.9, 18.6 MJ GE kg^{-1} DM respectively

[5] diet contained 29.7 gN and 17.6 MJ GE kg^{-1} DM

[6] biological value for growing rats

1.01 for Trials 1 and 2, suggesting that utilisation of some of the nucleic-acid nitrogen took place under circumstances of nitrogen paucity.

Nitrogen excretion rate at low nitrogen intake

Metabolic faecal nitrogen losses were 1.62 and 1.92 g day^{-1} for intakes of 5.3 and 6.9 g N day^{-1} in Trials 1 and 2. On the basis of feed intake, these values become 1.19 and 1.26 g N kg^{-1} DM consumed. D'Mello *et al* (1976) found metabolic faecal nitrogen losses on a protein-free diet to average 1.26 g N kg^{-1} DM consumed, while estimates of 1.14 (Armstrong and Mitchell, 1955) and 1.10 (Whiting and Bezeau, 1957) have also been derived directly on protein-deficient diets.

Corresponding values for endogenous urinary nitrogen losses in Trials 1 and 2 were 3.90 and 3.96 g day^{-1}. D'Mello *et al* (1976) using pigs of similar live weight give a value for EUN of 2.91 g N day^{-1}, similar to the figure of 3.2 g N day^{-1} obtained by Lubaszewska, Pastuszewska and Kielanowski (1973).

Total losses of nitrogen via faeces and urine were 5.52 and 5.88 g N day^{-1} or 283.1 and 282.7 mg N $kg^{-1}W^{0.75}$ day^{-1} for Trials 1 and 2 respectively. The standard for minimal obligatory nitrogen loss by growing pigs given adequate energy was set by Carr, Boorman and Cole (1977) at -150 mg N $kg^{-1}W^{0.75}$ day^{-1}. This value, like that of 133 mg N $kg^{-1}W^{0.734}$ proposed by Armstrong and Mitchell (1955), was estimated on a protein-free diet. With the intention of arriving at a figure for minimal obligatory nitrogen loss by two different methods (direct measurement on a protein-free diet and by extrapolation from a range of nitrogen intakes), Armstrong and Mitchell (1955) fed a low-protein diet to pigs of 35 kg live weight (average daily intake, 6.5 g N). It can be calculated from the original data that this diet engendered

nitrogen losses in the excreta of -300.4 mg N $kg^{-1}W^{0.75}$ day^{-1}, comparable losses to those obtained in Trials 1 and 2.

Daily nitrogen retentions obtained by nitrogen balance techniques

Nitrogen retentions on Diet 3, Trial 1 (intake 33.2 g N day^{-1}) and on Diet 2, Trial 2 (intake 31.0 g N day^{-1}) were 15.0 and 17.4 g day^{-1} respectively, in reasonable agreement with the nitrogen retention of 18.3 g day^{-1} measured for castrated male pigs between 20 and 70 kg live weight and assessed by comparative slaughter technique (Section 1). By retaining 114 g protein day^{-1}, of which 0.48 was incorporated in dissectible muscle mass, these appetite-fed pigs deposited 0.151 of their daily liveweight gain as crude protein. Thus, for nitrogen intakes of around 30 g day^{-1} it would appear that nitrogen retentions are equally valid whether derived by nitrogen balance or serial slaughter.

Difficulties in interpretation arise because of the nitrogen retention response to Diets 3 and 4 in Trial 2 (Figure 3.5). Common sense dictates that retentions on Diet 3 (nitrogen intake 60.4 g N day^{-1}) would surpass those on Diet 2 (intake 31.0 g N day^{-1}) to establish a "ceiling" value for nitrogen retention at prevailing levels of energy intake. Retentions obtained for Diet 4 (nitrogen intake 93.4 g N day^{-1}) should have been synonymous with those for Diet 3, that is, should have adhered to the established "ceiling". In practice, there was a larger margin between Diet 3 and Diet 4 retentions than existed between Diet 2 and Diet 3 retentions.

Examining the five balance periods in Trial 2 (Table 3.15), control pigs fed Diet 4 consistently retained 30-plus g N day^{-1}; extrapolation to crude protein deposition rate suggests 200 g protein deposited daily, a protein growth rate not approached by pigs of outstanding genetic potential. Boars fed to appetite (Section 1)

deposited 123 g whole body protein daily over the liveweight range 20 to 95 kg (55 to 165 days of age), representing 0.167 of daily live weight gain. Newcastle selected-line boars, also fed to appetite, deposited 138 g whole body protein day^{-1}, weight range 29 to 106 kg and 98 to 182 days of age, 0.15 of the daily liveweight increment (Henderson, Whittemore, Ellis, Smith and Laird, 1981). Boars in Section 1 directed 0.44 of protein gain to dissectible muscle, therefore as a 'rule of thumb', pigs of the age, sex and genotype to achieve maximum daily protein deposition rates retain 54 to 61 g protein day^{-1} in skeletal muscle and 69 to 77 g protein day^{-1} in other tissues such as skin, viscera and skeleton. Daily nitrogen retentions over 22 g day^{-1} are not substantiated by data from slaughter trials, nor should protein gains depart radically from 0.16 of daily liveweight gains.

Daily nitrogen retentions by pigs fed Diet 3, when extrapolated to crude protein gains, would account for 0.22 of liveweight gain. On an energy-expenditure basis, the nitrogen retention rate recorded for Diet 2 is acceptable: assuming the energy costs of lean and fat deposition to be 15 and 50 MJDE kg^{-1} respectively, 17.4 g N retained day^{-1} would require 22 MJDE day^{-1} (actual energy intake, 25 MJDE day^{-1}). However, the nitrogen retentions obtained on Diets 3 and 4 would depend on catabolism of body lipid reserves to supply requisite energy. Liveweight gains by pigs fed Diets 3 and 4 (0.62 and 0.69 kg day^{-1}, Table 3.20) give little indication of curtailment by nitrogen intake akin to that found for chicks fed supra-adequate protein diets (Fisher, Grun, Shapiro and Ashley, 1964): small reductions in body weight accompanied small, but consistent, additions to total carcass nitrogen (including feather nitrogen) compared with chicks fed diets containing adequate protein. Barber, Braude, Chamberlain and Mitchell (1964) measured a

response to higher protein levels in terms of nitrogen retention, but failed to detect a concommitant superiority in muscle content of the pig carcass at 60 kg. It is unlikely, therefore, that at higher nitrogen intakes the commercially-important skeletal muscle is the beneficiary of the extra nitrogen retained during catch-up protein growth. Boorman (1980) stated "increases in nitrogen are possible at more than adequate nitrogen intakes". Indication of the underlying mechanism integral to this phenomenon was provided by Golden *et al* (1977): recovered children reacted to higher than usual protein intakes by increasing their daily quota of protein retained as the product of a constant rate of protein synthesis and retarded rate of protein breakdown.

There is no reason for dismissing nitrogen retentions by pigs on Diet 4 as nonesense data. That said, it is unlikely that carcass lean represents the location in the body for extra protein deposition, or that elevated retention rates could be sustained long-term.

The concept of nitrogen stores

A change in nitrogen intake level from high to low nitrogen (treatments 3-1-3 and 1-3-1) caused negative nitrogen retentions in the 3-day balance following diet changeover. Retentions in the subsequent 7-day collection period were narrowly positive. This effect was more pronounced for pigs on treatment 3-1-3 than for pigs on treatment 1-3-1, the former having been fed on the high-protein diet for 17 days before the change to low protein while the latter received the high protein diet for 11 days prior to the change. Holt, Halac and Kajdi (1962) found that in the early days on a protein-free diet, rats previously fed on a high-protein diet catabolised protein at a more rapid rate than rats previously fed on a normal level of protein.

This proposal was substantiated for pigs by Vaughan, Filer and Churella (1962): pigs fed on high-protein diets developed correspondingly greater rates of protein turnover, and were rendered less successful at coping with the immediate effects of sudden protein deprivation. Pigs changed from a moderate level of nitrogen intake to low nitrogen intake (treatments 2-1-2 and 1-2-1) were able to make a swifter adjustment to their protein turnover rate and remained in positive nitrogen balance following the change to a low-nitrogen diet. The modification to nitrogen excretion rate required by the sudden decrease in nitrogen intake was accomplished within 4 days of the diet change, such that urinary nitrogen output on treatments 3-1-3 and 1-3-1 averaged 5.45 (±0.783) g day^{-1} for the 3-day balance and 3.67 (±0.458) g day^{-1} for the 7-day balance, a reduction in urinary nitrogen excretion of 0.33; corresponding figures for treatments 2-1-2 and 1-2-1 were 4.19 (±0.278) g day^{-1} in the 3-day balance and 3.75 (±0.224) g day^{-1} in the 7-day balance, a reduction of 0.11. It took 30 hours for rats changed from a high- to a low-protein diet to decrease urinary nitrogen output by 0.50 (Das and Waterlow, 1974). For Trial 1, the adaptation in nitrogen output consequent upon feeding the low-nitrogen diet (Diet 1) would have been more or less completed during the two-day prefeeding period. If compensation merely entails the repletion of depleted labile protein reserves, rather than catch-up muscle protein growth, then the advantage of compensating pigs over control pigs would dwindle to zero once the labile protein stores were replenished. Evidence for a mechanism of this type was provided in Trial 2 by pigs realimented on the very high nitrogen diet (treatment 1-4-4) and those given high nitrogen after a period at moderate nitrogen intake (treatment 2-3-3) (Figures 3.8 and 3.9). The initial elevations

in nitrogen retention over respective controls' retentions (4.29 g N day^{-1} for 1-4-4 and 6.32 g N day^{-1} for 2-3-3, balance period 2B) were insignificant in magnitude by balance period 3B, that is, within 15 days of the change to higher nitrogen.

Compensatory nitrogen retention

In Trial 2, extra nitrogen retentions were significant for the treatments involving combinations of Diets 1 and 3 only, and were maintained over the entire 22-day realimentation period in the case of treatment 1-3-3 (9.85 g extra N in balance period 2B, 9.34 extra N in balance period 3B; $P < 0.05$). However, the increases in efficiency of nitrogen utilisation and biological value produced, although considerable, were not significant in either balance period. The fact that enhanced nitrogen retentions were maintained for 22 days (treatment 1-3, Trial 1 and treatment 1-3-3, Trial 2) is indicative of a more profound alteration in protein metabolism than the temporary shut-down of the urea cycle. In rats, the latter was reversed shortly after the commencement of refeeding (Das and Waterlow, 1974; Figure 3.2), so that its contributions to protein flux would be resumed within 2 days. Reduction of the overall rate of protein flux in pigs fed Diet 1, Trial 1 for 12 days and in pigs fed Diet 1, Trial 2 for 10 or 17 days is unlikely to have occurred for two reasons. First, it took 35 days on a low-protein diet to reduce flux rate by 0.50 (Waterlow and Stephen, 1967), whereas after 10 days on this diet flux rate was virtually unchanged. Thus the periods of low-nitrogen intake employed in the present trials can not have represented the same threat to the integrity of the protein flux as a more prolonged or more severe (protein-free diet) deficiency. Second, endogenous urinary nitrogen losses did not alter appreciably in magnitude over time on test in either trial (Tables 3.7 and 3.13).

A depression in flux rate brought about by continued nitrogen shortage would have been expected to progressively diminish EUN loss.

SUMMARY

Enhanced nitrogen retentions were demonstrated in both trials. After a period of nitrogen deprivation, refed pigs retained more nitrogen than control pigs fed the same diet. This response was obtained whenever pigs were changed from low nitrogen intake to a higher nitrogen intake. However, the amount of extra nitrogen retained was not always significantly higher than that retained by control pigs. As a general rule, the more generous the nitrogen supply during rehabilitation, the more precipitate the decline in compensatory response. Presumably refed pigs given high nitrogen intakes quickly adopt the high protein turnover rates such diets induce, and are "profligate" in their usage of nitrogen as a result.

The ability of pigs to produce the compensatory response stems from the reduction in nitrogen excretion rate (allied to reduced protein synthesis and breakdown rates) caused by nitrogen deprivation being "carried over" into the refeeding phase. Hence, for a time, nitrogen output is not representative of nitrogen intake. Reduction in nitrogen output, mediated through a decrease in the proportion of the flux excreted (by temporary shutting-down of the urea cycle) would account for the enhanced nitrogen retentions recorded during early refeeding; three-day balance retentions did not convincingly exceed 7-day balance retentions, that is, the immediate response to higher nitrogen was not more pronounced than the longer-term response to increased nitrogen supply. Elevation in nitrogen retained in the two to four days following the diet changeover could represent the lag in urinary nitrogen output

and urea cycle enzyme activities before these returned to values appropriate to the higher-nitrogen diet. The longer-term advantage in nitrogen retention, persisting after 4 days from diet changeover, might have been the outcome of more efficient utilisation of absorbed nitrogen (recovering children used a higher proportion of nitrogen entering the metabolic pool for protein synthesis and practised a greater degree of recycling of amino-acids freed during protein breakdown), or might signal the exploitation of a wider spectrum of constituents in the dried microbial cell protein source. A third possibility is that more efficient utilisation of nitrogen was achieved by a combination of these two mechanisms.

The occurrence of the compensatory response at very high nitrogen intake (Diet 4, Trial 2) suggests the phenomenon under investigation to be of greater relevance to the replenishment of labile protein reserves than to catch-up protein gains in muscle. As labile protein stores are likely to be located in tissues which are not of primary commercial value, the compensatory nitrogen retention response would not lend itself to successful exploitation in practical husbandry terms. Indeed, nitrogen deprivation in younger pigs (possessing smaller depletable protein reserves), carried out over a sufficiently lengthy period to curtail muscle growth, would almost certainly result in persistent retardation of muscle gain: catch-up protein gains were not demonstrated by the experiment described in Section 2C.

CONCLUDING REMARKS

The following points are suggested by the preceding studies on protein growth:

SECTION I

(i) The form of the relationship between daily protein or lean deposition and age or live weight is neither quadratic nor constant from weaning to virtual maturity. It appears to conform more or less to a plateau, achievable at 20 kg live weight and sustainable until 100 kg live weight and beyond. The rate of decline in daily protein and lean gain is influenced by sex and genotype, with entire males and later-maturing pigs exhibiting a more gradual decrease in protein growth between 110 and 190 kg live weight. The rate of increase in daily protein accretion is conditioned by voluntary feed intake which explains the early, and short-lived, advantage of castrates over boars in protein growth rate.

(ii) Daily feed intakes traced a similar pattern to daily protein deposition; that is, a steep, linear increase to peak intake followed by a plateau, about which there was considerable day-to-day variation. Peak feed intakes of around 4.5 kg day^{-1} and plateau daily intakes (3.97, 3.63 and 3.74 kg day^{-1} for boars, gilts and castrates respectively) were demonstrably higher than other values in the literature for pigs of similar weight; the age and live weight at which peak intake was reached (140 days and 85 kg) are confirmed elsewhere. However, it was particularly in the middle range of live weights, 20 to 60 kg that increase in daily intake was higher than usual, suggesting considerable reserves of appetite potential, and hence, protein growth potential.

(iii) Protein content of the empty body was relatively stable at 0.144 for boars and gilts and 0.124 for castrates. Dissected lean comprised 0.305 of the empty body and 2.21 x total body protein, irrespective of sex, age or live weight of pig.

(iv) Estimated daily energy requirement for maintenance per kg metabolic body weight, 0.545 MJ, was rather greater than expected. The value for k_p, 0.27, was lower than previous estimates but is perfectly valid considering the range of live weights used and the generally low efficiency of gains (average feed conversion ratios were 3.69 for boars, 3.66 for gilts and 4.13 for castrates). Indeed, it might be argued that k_p should have been still lower and that the seemingly exaggerated ME_M requirement includes some of the increase in energy cost of protein deposition accompanying increase in live weight. Efficiency of energy utilisation for lipid deposition, 0.73, indicates this parameter to be independent of age or size of pig.

SECTION II

(v) Recovery from the post-weaning growth check is accelerated by offering young pigs diets of high nutrient density and ingredient quality which are also stimulatory to appetite.

(vi) During the first six days following weaning, lipid is mobilised from the empty body at a rate of approximately 36 g day^{-1}. The greatest contribution to lipid mobilisation comes from carcass fatty tissue, the subcutaneous fat depot. Carcass muscle plus bone, and to a lesser extent, the non-carcass fraction, are relatively protected during intake depression and continue to increase in mass, albeit at a reduced rate.

(vii) Imposed feed restrictions, both severe and prolonged and mild and short-lived, did not lead to significant augmentation of daily protein gains once the intake restriction was rescinded and the expression of appetite permitted. Refed pigs did not consume more food than appetite-fed controls, whether on an absolute basis or in terms of intake per kg body weight. Daily protein deposition was similar to that in controls of the same age and live weight, but there was some suggestion of enhanced lipid deposition relative to controls of the same weight. Neither the mild nor the severe intake restriction resulted in greater overall efficiency of food utilisation for growth.

(viii) Young female pigs fed to appetite between 25 and 70 days deposited an average of 80 g protein daily on a mean body weight of 16 kg. This deposition rate comprised 0.74 of the average daily protein gained by female pigs between 20 and 150 kg (108 g day^{-1}) and 0.65 of the maximum daily protein accretion rate measured for gilts in Section I (0.123). Thus at 0.07 of mature live weight, pigs were capable of achieving between two-thirds and three-quarters of maximum daily protein deposition, further proof that the plateau in daily deposition rate could have been reached by 20 kg live weight.

(ix) Feeding of inferior quality diets to early-weaned pigs will delay growth (offset the growth curve) irrevocably. Unless troubled by post-weaning scours, it is a false economy to restrict the intake of young pigs or to proffer unappetising diets containing low quality protein and of reduced digestibility.

SECTION III

(x) Despite the failure of the serial slaughter trial to detect enhanced protein gains following intake restriction, the evidence from nitrogen balance trials indicated that a compensatory nitrogen response does exist. Pigs possess a physiological mechanism whereby they are able to become more efficient in their utilisation of protein when protein intake is curtailed. This response involves a reduction in amount of nitrogen excreted in the urine (probably consequent upon the limitation of the proportion of the protein flux that is excreted) and in association with contraction of protein synthesis and breakdown rates. During early refeeding the pig maintains, for a time, the reduced level of nitrogen output. Later in the refeeding phase, compensation appears to be sustained by enhanced efficiency of utilisation of absorbed nitrogen (possibly by the re-cycling of amino-acids released by protein degradation) and exploitation of a wider spectrum of nitrogen components in the protein source (for example, nucleic-acid nitrogen in 'Pruteen').

(xi) Extra nitrogen retained during compensation was 2.73-4.20 g day^{-1}, and it was demonstrated that elevated nitrogen retention can be maintained for over 20 days.

(xii) The rapid disappearance of the compensatory response when, in the course of refeeding, very high or high nitrogen intakes followed low or moderate nitrogen intake, suggests that compensation is concerned with replenishment of labile protein reserves rather than the promotion of protein deposition in skeletal muscle. Furthermore, nitrogen retentions at high nitrogen intakes were too high for a considerable proportion of the protein retained to be directed to lean mass; bearing in mind the relatively inviolate status of body muscle where

intake is compromising to the animal, it is likely that locations other than skeletal muscle would take priority during repletion. It therefore remains to be demonstrated that compensatory nitrogen retention is of any commercial consequence, notwithstanding its undoubted biological significance for the pig.

NEXT EXPERIMENTS

a) trials with young pigs should be concerned with further maximisation of feed intake, rather than dwelling, as hitherto, on precise combinations of energy and protein levels in weaner diets. However, high quality dietary ingredients are of importance, as these generally comprise the feed constituents which help to increase palatability. An element of force feeding in intake studies might help to clarify the issue of maximum daily feed intake for age and live weight. Furthermore, attention should centre upon methods of weaning to mitigate the intake-induced growth depression consequent upon removal from the sow; for example, gradual weaning (reduced frequency of sucklings) may be of some merit.

b) Slaughter experiments could be used to establish the most expedient slaughter weights for entire males and later-maturing pigs to exploit to the full their greater protein deposition potential; results from my experiment suggest 100-110 kg live weight as a suitable slaughter weight for entire males.

c) Selection for increased daily protein or lean deposition rate should favour those pigs exhibiting exceptional daily protein and lean gains relative to contemporaries, and which also deposit tissues with a low lipid : protein ratio. Such animals would reap benefits to the producer

in terms of lean tissue conversion ratio. It would be desirable for selected pigs to retain sizable appetites in order to achieve rapid increase in daily protein and lean deposition at younger ages and lower live weights. Selection should avoid animals which preferentially partition energy to heat production.

d) Quantification of protein and lean mass at maturity of selected pigs would facilitate greater accuracy in prediction of daily protein and lean gains and would place the rationing of improved breeding stock on a sounder basis. Cull animals are not suitable for this study as illness, feed restriction and the demands of successive breeding cycles may prejudice the attainment of representative protein and lean masses at maturity.

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APPENDIX 1.1: Live weight and empty body weight at slaughter and chemical composition of the empty body

Litter	Sex	Age at slaughter (days)	Live weight at slaughter (kg)	Empty body weight at slaughter (kg)	Chemical composition of empty body: dry matter (kg)	water (kg)	protein (kg)	lipid (kg)	ash (kg)	gross energy (MJ)
1	B	52	22.70	20.81	6.954	13.13	3.383	2.564	0.704	181.74
1	G	52	24.62	22.88	7.308	13.96	3.682	2.648	0.721	191.80
1	C	52	22.17	20.09	6.436	12.75	3.413	2.004	0.765	160.96
2	B	55	13.20	12.18	3.493	7.30	2.067	0.863	0.462	84.42
2	G	55	16.46	15.03	4.708	9.18	2.405	1.309	0.544	118.25
2	C	55	21.00	19.39	6.150	12.78	3.384	1.964	0.664	169.55
3	B	91	43.80	41.96	14.784	25.74	7.688	5.309	1.600	392.68
3	G	91	44.10	41.77	13.887	24.34	6.620	5.557	1.454	376.14
3	C	91	45.20	42.41	15.388	25.28	7.449	6.080	1.560	397.31
4	B	91	44.70	41.55	12.685	26.79	7.387	3.324	1.731	305.01
4	G	91	32.60	30.18	9.980	17.90	5.361	3.358	1.124	258.52
4	C	91	50.40	46.34	16.457	25.05	7.932	6.762	1.713	455.07
5	B	123	74.20	70.97	30.747	32.16	11.240	16.244	2.485	900.16*
5	G	123	69.00	66.25	28.604	32.42	10.831	13.297	2.313	775.68*
5	C	123	75.60	71.69	29.084	29.44	9.636	16.576	2.251	868.30*
6	B	123	85.15	80.34	34.761	39.33	14.050	17.532	2.977	1019.19*
6	G	123	67.60	63.78	28.091	30.07	9.681	15.653	2.084	823.90*
6	C	123	74.90	71.27	29.731	33.50	11.323	15.090	2.448	851.27*
7	B	124	70.04	66.55	25.069	31.91	10.714	11.337	2.323	700.85*
7	G	124	73.50	69.91	33.965	31.47	10.794	19.762	2.425	1019.76*
7	C	124	72.40	68.86	30.769	30.89	11.016	16.070	2.759	877.83*
8	B	126	71.50	68.12	31.769	32.31	10.540	17.898	2.550	947.27*
8	G	126	69.40	66.26	28.334	29.78	10.526	15.140	2.497	839.82*
9	G	163	110.80	106.95	55.329	49.30	16.216	35.100	3.830	1810.69
9	C	163	111.90	107.50	59.650	47.16	15.448	39.377	3.968	1892.52
10	B	165	95.30	91.55	37.739	51.51	16.187	18.215	3.108	1076.98
10	G	165	104.10	98.42	43.529	49.72	15.388	24.519	3.111	1379.57
10	C	165	104.00	98.00	47.716	49.22	15.392	28.223	3.392	1471.78
11	B	195	150.13	142.83	63.255	75.02	26.467	30.019	5.295	1799.18
11	G	195	136.30	131.80	69.393	59.06	20.518	43.453	4.452	2176.51
11	C	195	150.06	144.11	77.327	65.20	22.084	49.474	5.270	2473.57
12	B	231	163.30	155.64	77.287	72.09	24.902	46.412	5.254	2412.81
12	G	231	164.60	158.22	90.231	61.80	20.147	64.300	4.429	2992.95
12	C	231	135.80	130.93	76.376	49.13	15.876	56.966	3.413	2605.89
13	B	285	200.03	193.70	91.579	81.86	27.443	56.082	5.548	2835.83
13	C	285	149.50	145.20	77.722	60.38	19.780	51.850	4.422	2622.61
14	B	330	199.60	192.12	98.341	82.90	29.627	61.170	5.627	3104.57
14	G	330	182.30	177.37	94.345	74.78	24.602	62.403	5.034	3039.43
14	C	330	217.30	207.70	112.107	86.33	28.156	76.325	6.629	3617.86
15	B	332	205.20	195.80	99.338	87.14	29.769	61.127	6.098	3082.71
15	G	332	205.80	198.50	112.685	86.32	28.217	76.566	5.734	3678.97
15	C	332	198.90	191.90	117.178	70.76	23.529	86.996	4.632	3945.41

B = boar; G = gilt; C = castrate *exclusive of blood GE

APPENDIX 1.2: Weight of dissected lean and weight and chemical composition of dissected lean plus intermuscular fat (IMF)

Litter	Sex	Age at slaughter (days)	Weight of dissected lean (kg)	Weight of dissected lean + IMF (kg)	Chemical composition of dissected lean plus intermuscular fat: dry matter (kg)	water (kg)	protein (kg)	ash (kg)	lipid (kg)	gross energy (MJ)
1	B	52	7.966	9.414	2.792	6.62	1.668	0.101	0.918	75.45
1	G	52	8.476	9.830	2.929	6.90	1.935	0.110	0.845	77.87
1	C	52	8.012	9.278	2.669	6.61	1.830	0.107	0.706	70.93
2	B	55	4.060	4.612	1.325	3.29	0.977	0.060	0.281	34.09
2	G	55	5.620	6.166	1.701	4.47	1.174	0.073	0.402	43.07
2	C	55	7.448	8.266	2.294	5.97	1.616	0.116	0.552	59.84
3	B	91	15.920	19.112	6.060	13.05	3.775	0.244	2.060	170.04
3	G	91	16.660	18.948	5.811	13.14	3.478	0.204	2.031	163.45
3	C	91	16.644	20.224	6.508	13.72	4.079	0.249	2.119	177.70
4	B	91	16.702	18.854	5.104	13.75	3.643	0.213	1.217	133.83
4	G	91	11.040	13.198	3.986	9.21	2.809	0.157	1.057	107.83
4	C	91	18.248	21.112	6.350	14.76	4.177	0.233	2.142	182.73
5	B	123	22.036	27.248	10.561	16.69	5.648	0.296	4.201	298.39
5	G	123	21.623	27.927	9.444	18.48	5.854	0.451	3.783	258.04
5	C	123	20.518	27.294	10.254	17.04	5.104	0.298	4.622	299.28
6	B	123	30.838	37.746	14.589	23.16	7.465	0.444	6.256	412.28
6	G	123	19.926	25.058	9.046	16.01	4.943	0.349	3.535	252.40
6	C	123	24.485	30.150	11.143	19.01	6.155	0.337	4.127	307.14
7	B	124	24.278	27.858	9.651	18.21	5.973	0.330	3.250	268.70
7	G	124	22.036	28.396	11.276	17.12	5.494	0.331	5.029	327.29
7	C	124	21.016	26.306	10.296	16.01	5.169	0.281	4.436	290.93
8	B	126	22.492	29.788	11.249	18.54	5.522	0.321	4.971	325.68
8	G	126	24.278	28.666	11.326	17.34	5.818	0.339	4.765	330.55
9	G	163	35.270	47.778	19.140	28.64	9.087	0.435	9.608	607.57
9	C	163	33.308	48.032	20.178	27.85	8.652	0.485	10.969	646.64
10	B	165	39.564	46.082	15.907	30.18	9.271	0.474	6.127	454.60
10	G	165	37.036	44.874	16.251	28.62	8.479	0.452	7.131	475.97
10	C	165	35.282	44.096	15.577	28.52	8.565	0.467	6.126	442.90
11	B	195	55.068	68.606	24.147	44.46	14.977	0.700	8.514	688.07
11	G	195	47.112	63.106	27.515	35.59	11.185	0.583	15.929	889.99
11	C	195	50.864	67.868	27.915	39.95	12.539	0.586	14.572	886.82
12	B	231	48.676	69.130	29.574	39.56	13.046	0.674	15.917	933.41
12	G	231	44.188	64.958	30.853	34.10	10.222	0.502	19.650	1006.13
12	C	231	32.940	53.288	25.711	27.58	8.915	0.443	16.517	839.02
13	B	285	58.952	81.052	31.002	50.05	14.536	0.731	14.952	930.70
13	C	285	46.324	63.944	26.503	37.44	11.133	0.558	14.477	831.71
14	B	330	66.944	78.724	28.689	50.04	14.923	0.704	12.698	851.25
14	G	330	56.348	79.114	32.642	46.47	14.044	0.678	17.313	1005.22
14	C	330	60.676	87.256	39.755	47.50	15.827	0.739	23.105	1254.49
15	B	332	64.038	83.362	33.178	50.18	15.243	0.716	16.984	1027.25
15	G	332	67.312	91.248	39.071	55.18	15.780	0.734	21.876	1232.07
15	C	332	53.698	74.992	32.743	42.25	13.038	0.585	18.372	1029.67

APPENDIX 1.3: Weight and chemical composition of carcass subcutaneous fat and skin

				Subcutaneous fat:							Skin:						
Litter	Sex	Age at slaughter (days)	*P2 Backfat depth (mm)*	weight (kg)	DM (kg)	water (kg)	protein (kg)	ash (kg)	lipid (kg)	GE (MJ)	weight (kg)	DM (kg)	water (kg)	protein (kg)	ash (kg)	lipid (kg)	GE (MJ)
1	B	52	*4.5*	1.620	1.103	0.59	0.161	0.007	0.934	40.50	0.872	0.390	0.48	0.242	0.007	0.151	10.81
1	G	52	*5*	1.638	1.177	0.46	0.132	0.005	1.040	44.01	0.880	0.392	0.49	0.207	0.008	0.153	10.90
1	C	52	*4.5*	1.348	0.850	0.50	0.149	0.007	0.696	30.88	0.854	0.366	0.49	0.218	0.006	0.135	10.45
2	B	55	*5*	0.666	0.374	0.29	0.082	0.005	0.284	13.11	0.502	0.206	0.30	0.136	0.005	0.057	5.46
2	G	55	*4.5*	0.946	0.585	0.36	0.111	0.007	0.469	21.03	0.584	0.300	0.28	0.170	0.006	0.125	17.39
2	C	55	*4.5*	1.492	0.925	0.57	0.142	0.006	0.777	30.21	0.870	0.347	0.52	0.217	0.007	0.126	24.35
3	B	91	*5*	1.986	1.641	0.35	0.121	0.006	1.523	62.71	3.376	1.812	1.56	1.228	0.032	0.566	51.21
3	G	91	*5*	2.798	2.007	0.79	0.289	0.013	1.703	73.76	1.892	1.019	0.87	0.522	0.013	0.467	29.69
3	C	91	*6*	2.896	2.139	0.76	0.178	0.040	1.940	60.43	2.084	1.024	1.06	0.575	0.019	0.391	28.93
4	B	91	*5*	1.820	1.063	0.76	0.226	0.013	0.821	37.57	1.916	0.862	1.05	0.635	0.017	0.202	22.93
4	G	91	*4.5*	1.376	0.978	0.40	0.120	0.006	0.846	35.90	1.564	0.901	0.66	0.342	0.012	0.552	26.84
4	C	91	*9*	4.114	3.038	1.08	0.265	0.019	2.764	114.91	2.160	1.197	0.96	0.746	0.020	0.375	32.33
5	B	123	*17*	10.064	8.883	1.18	0.455	0.013	8.583	348.05	1.734	1.372	0.36	1.046	0.020	0.358	34.25
5	G	123	*18*	9.280	7.656	1.62	0.776	0.027	6.850	287.49	1.412	1.059	0.35	0.818	0.018	0.236	26.23
5	C	123	*22*	9.622	8.290	1.33	0.512	0.016	7.840	320.19	1.536	1.340	0.20	0.752	0.017	0.579	34.24
6	B	123	*16*	9.428	8.160	1.27	0.502	0.018	7.702	314.54	2.286	1.865	0.42	1.386	0.027	0.490	45.63
6	G	123	*17*	10.406	9.078	1.33	0.519	0.016	8.516	346.93	1.598	1.313	0.29	0.809	0.017	0.352	25.07
6	C	123	*26*	8.352	7.483	0.87	0.509	0.019	7.030	288.28	1.630	1.290	0.34	0.910	0.017	0.446	31.13
7	B	124	*15*	5.960	5.395	0.57	0.228	0.005	5.182	209.05	1.530	1.159	0.37	0.573	0.012	0.536	29.59
7	G	124	*21*	13.166	11.447	1.72	0.594	0.028	10.880	441.59	2.062	1.860	0.20	0.906	0.017	0.907	45.34
7	C	124	*22*	9.112	7.991	1.12	0.398	0.022	7.544	305.89	1.978	1.611	0.37	1.158	0.024	0.387	39.24
8	B	126	*25*	10.632	9.694	0.94	0.383	0.019	9.460	380.81	1.652	1.417	0.24	0.996	0.016	0.449	34.83
8	G	126	*18*	8.544	7.551	0.99	0.397	0.022	7.168	291.08	1.796	1.429	0.37	1.021	0.021	0.375	35.53
9	G	163	*24*	22.412	19.675	2.74	0.484	0.067	19.066	760.74	3.802	2.097	1.71	1.480	0.021	0.518	55.30
9	C	163	*27*	24.856	22.131	2.46	0.500	0.059	21.582	830.55	2.696	1.690	1.01	0.988	0.017	0.631	41.16
10	B	165	*15*	8.584	7.060	1.52	0.427	0.005	6.574	271.45	3.896	1.687	2.21	1.407	0.022	0.258	43.36
10	G	165	*17*	14.516	12.394	2.12	0.512	0.026	11.863	480.79	3.408	1.562	1.85	1.238	0.020	0.290	40.60
10	C	165	*23*	17.620	15.518	2.10	0.607	0.027	15.067	606.45	3.048	1.487	1.56	1.215	0.038	0.272	39.39
11	B	195	*21*	18.654	15.580	3.07	0.816	0.063	14.114	573.93	5.880	4.055	1.83	3.376	0.044	0.488	98.86
11	G	195	*26*	22.416	20.126	2.29	0.659	0.061	19.160	748.83	4.740	3.330	1.41	2.584	0.034	0.562	83.09
11	C	195	*37*	29.642	26.619	3.02	0.852	0.094	26.059	1044.21	4.164	2.568	1.60	2.016	0.027	0.546	61.33
12	B	231	*35*	30.056	24.204	5.85	1.623	0.074	22.638	946.50	6.980	4.052	2.93	3.084	0.038	0.708	100.60
12	G	231	*45*	40.644	35.564	5.08	0.967	0.029	34.451	1377.00	5.728	3.737	1.99	2.173	0.036	1.435	115.89
12	C	231	*38*	34.458	31.277	3.18	0.899	0.011	30.239	1202.40	3.928	2.540	1.39	1.226	0.012	1.187	75.60
13	B	285	*44*	36.208	31.465	4.74	1.078	0.042	29.750	1194.62	7.692	4.877	2.82	3.741	0.051	1.008	127.90
13	C	285	*37*	30.970	28.062	2.91	0.900	0.044	27.142	1087.93	3.926	2.646	1.28	1.540	0.021	1.111	74.37
14	B	330	*38*	42.092	36.614	5.48	1.792	0.033	34.520	1398.93	9.954	5.661	2.03	3.797	0.040	1.857	151.00
14	G	330	*36*	37.758	34.199	3.56	1.259	0.019	32.648	1312.77	6.074	3.694	2.38	1.983	0.020	1.534	107.09
14	C	330	*52*	48.990	38.321	10.67	1.459	0.039	36.696	1463.12	6.400	4.040	2.36	2.602	0.026	1.241	110.17
15	B	332	*35*	32.790	28.655	4.14	1.148	0.028	27.374	1102.92	8.448	5.525	2.92	3.688	0.026	1.610	150.32
15	G	332	*45*	45.020	40.949	4.07	1.282	0.014	39.839	1596.05	6.808	4.853	1.96	2.867	0.027	1.680	133.77
15	C	332	*50*	52.208	47.676	4.53	1.162	0.034	46.475	1834.94	5.636	3.950	1.69	2.112	0.021	2.030	111.06

APPENDIX 1.4: Weights and chemical composition of carcass bone and blood

			Carcass bone:							Blood:						
Litter	Sex	Age at slaughter (days)	weight (kg)	DM (kg)	water (kg)	protein (kg)	ash (kg)	lipid (g)	GE (MJ)	weight (kg)	DM (kg)	water (kg)	protein (kg)	ash (kg)	lipid (kg)	GE (MJ)
1	B	52	1.936	0.913	1.02	0.348	0.379	0.126	13.17	0.50	0.089	0.41	0.081	0.005	0.60	2.05
1	G	52	2.010	0.893	1.12	0.354	0.372	0.110	12.66	0.98	0.168	0.81	0.155	0.009	1.08	3.94
1	C	52	1.938	0.901	1.04	0.346	0.369	0.118	12.82	0.45	0.081	0.37	0.077	0.004	0.75	1.89
2	B	55	1.202	0.519	0.68	0.236	0.208	0.059	7.87	0.20	0.034	0.17	0.032	0.002	0.24	0.80
2	G	55	1.390	0.618	0.77	0.253	0.274	0.072	8.79	0.40	0.070	0.33	0.066	0.004	0.36	1.65
2	C	55	1.895	0.847	1.05	0.381	0.323	0.114	13.48	0.45	0.078	0.37	0.075	0.004	0.62	1.80
3	B	91	4.416	2.211	2.20	0.821	0.887	0.412	35.57	1.52	0.291	1.22	0.269	0.012	2.79	6.85
3	G	91	3.932	2.006	1.93	0.734	0.832	0.361	31.50	1.22	0.269	0.94	0.254	0.013	1.94	6.39
3	C	91	3.692	1.915	1.78	0.692	0.710	0.425	33.02	1.57	0.323	1.25	0.295	0.016	2.07	7.64
4	B	91	4.168	2.142	2.03	0.852	0.947	0.237	28.02	1.38	0.323	1.06	0.315	0.014	2.45	7.73
4	G	91	2.958	1.459	1.50	0.613	0.584	0.212	22.78	0.87	0.190	0.68	0.175	0.008	1.07	4.54
4	C	91	3.990	2.173	1.82	0.775	0.950	0.373	32.95	1.25	0.272	0.98	0.261	0.012	2.17	6.40
5	B	123	4.602	2.910	1.69	0.979	1.347	0.482	40.87	1.85	0.401	1.45	0.404	0.017	1.92	ND
5	G	123	4.258	2.607	1.65	0.933	1.166	0.391	36.78	1.74	0.356	1.38	0.349	0.018	1.72	ND
5	C	123	4.614	2.851	1.76	0.938	1.132	0.636	46.55	1.18	0.236	0.94	0.233	0.012	0.94	ND
6	B	123	5.412	3.371	2.04	1.075	1.511	0.622	49.83	2.69	0.533	2.16	0.540	0.028	1.71	ND
6	G	123	3.810	2.418	1.39	0.860	1.047	0.648	35.17	1.67	0.325	1.34	0.321	0.017	1.17	ND
6	C	123	4.758	2.876	1.88	1.038	1.280	0.500	43.62	2.01	0.403	1.61	0.400	0.022	1.93	ND
7	B	124	4.802	3.055	1.75	1.011	1.190	0.672	50.27	1.14	0.275	0.86	0.266	0.012	2.86	ND
7	G	124	4.724	2.905	1.82	0.907	1.224	0.641	46.58	2.06	0.551	1.51	0.532	0.023	3.75	ND
7	C	124	5.286	3.248	2.04	1.149	1.272	0.661	53.10	1.23	0.299	0.93	0.301	0.014	1.79	ND
8	B	126	5.310	3.283	2.03	1.055	1.435	0.573	47.44	1.32	0.254	1.07	0.251	0.013	1.02	ND
8	G	126	4.666	2.875	1.79	0.923	1.323	0.533	41.82	1.50	0.319	1.18	0.316	0.015	1.53	ND
9	G	163	7.502	4.714	2.79	1.447	2.076	1.037	69.31	3.10	0.757	2.34	0.719	0.030	5.75	18.20
9	C	163	8.298	5.239	3.06	1.668	2.198	1.295	78.41	2.64	0.593	2.05	0.556	0.026	4.27	13.96
10	B	165	7.877	4.381	3.50	1.424	1.663	1.063	73.63	3.10	0.663	2.44	0.602	0.032	4.24	15.72
10	G	165	7.274	4.257	3.02	1.318	1.677	1.122	69.88	3.35	0.714	2.64	0.674	0.035	4.00	17.02
10	C	165	7.838	4.604	3.23	1.388	1.808	1.298	69.41	3.35	0.764	2.59	0.706	0.035	6.11	18.32
11	B	195	10.478	6.491	3.99	2.102	2.811	1.345	96.62	5.60	0.982	4.62	0.895	0.051	8.25	23.05
11	G	195	9.400	6.077	3.32	1.901	2.614	1.269	91.57	4.10	0.962	3.14	0.901	0.040	5.77	22.77
11	C	195	10.900	7.036	3.86	2.272	3.116	1.508	96.21	4.40	1.024	3.38	0.976	0.042	6.15	24.39
12	B	231	10.742	6.655	4.09	2.067	2.868	1.531	91.29	5.18	1.124	4.06	1.018	0.050	9.89	26.75
12	G	231	10.226	6.364	3.86	1.956	2.655	1.614	97.39	4.45	1.110	3.34	1.049	0.042	6.22	26.35
12	C	231	7.596	4.840	2.76	1.504	1.968	1.322	77.37	3.22	0.651	2.57	0.584	0.028	6.51	15.49
13	B	285	11.382	7.264	4.12	2.322	2.953	1.891	110.96	4.28	0.940	3.34	0.885	0.043	7.52	22.30
13	C	285	9.554	6.393	3.16	1.745	2.453	1.983	96.70	4.34	0.948	3.39	0.911	0.043	6.82	22.54
14	B	330	12.832	8.397	4.43	2.445	3.134	2.737	149.78	5.47	1.169	4.30	1.109	0.052	6.55	27.75
14	G	330	11.570	7.567	4.00	2.164	2.924	1.867	120.82	5.26	1.283	3.98	1.267	0.051	8.21	30.70
14	C	330	14.008	9.349	4.66	2.697	3.744	3.078	138.76	5.84	1.165	4.67	1.089	0.170	11.65	27.64
15	B	332	13.838	9.056	4.78	2.979	3.766	1.971	108.18	6.60	1.650	4.95	1.568	0.067	11.22	39.51
15	G	332	12.634	8.338	4.30	2.474	3.181	2.191	129.51	6.50	1.503	5.00	1.452	0.069	9.02	35.59
15	C	332	10.618	7.288	3.33	2.173	2.773	1.896	125.81	6.52	1.298	5.22	1.205	0.065	8.31	31.04

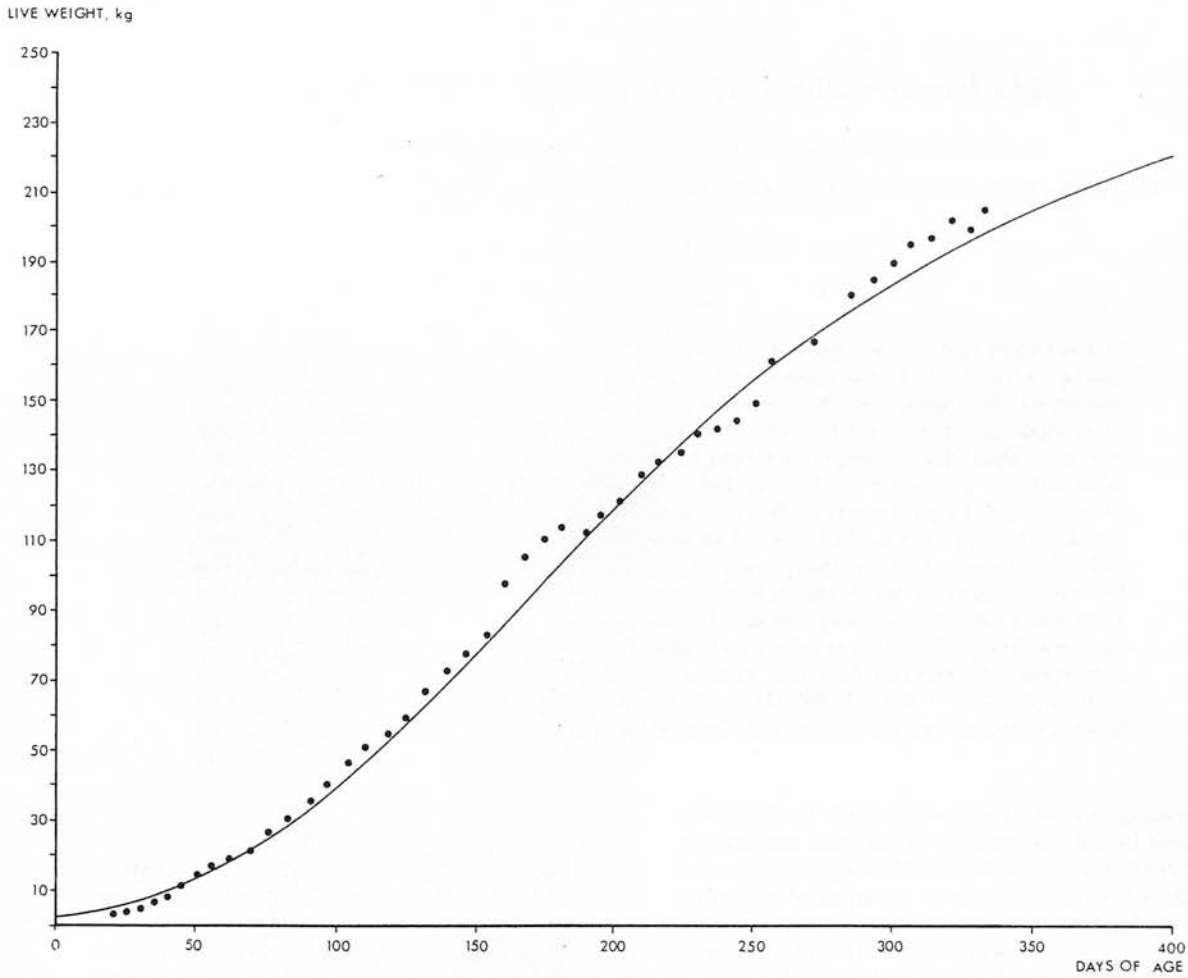
ND = not determined

APPENDIX 1.5: Weights and chemical composition of the non-carcass (NC) and head, feet and tail (HFT) fractions

			Non-carcass:							Head, feet, tail:						
Litter	Sex	Age at slaughter (days)	weight (kg)	DM (kg)	water (kg)	protein (kg)	ash (kg)	lipid (kg)	GE (kg)	weight (kg)	DM (kg)	water (kg)	protein (kg)	ash (kg)	lipid (kg)	GE (kg)
1	B	52	2.995	0.649	2.35	0.434	0.046	0.076	15.81	2.675	1.018	1.66	0.449	0.159	0.358	23.95
1	G	52	3.220	0.699	2.52	0.447	0.038	0.107	17.36	2.710	1.050	1.66	0.452	0.179	0.392	25.06
1	C	52	2.775	0.590	2.19	0.378	0.040	0.082	14.57	2.525	0.979	1.55	0.415	0.232	0.266	19.42
2	B	55	2.010	0.439	1.57	0.299	0.028	0.052	10.77	1.595	0.596	1.00	0.305	0.154	0.130	12.32
2	G	55	2.320	0.493	1.83	0.334	0.031	0.060	12.19	1.795	0.657	1.14	0.297	0.149	0.181	14.13
2	C	55	3.682	0.788	2.89	0.526	0.049	0.109	19.39	2.280	0.871	1.41	0.427	0.159	0.285	20.48
3	B	91	6.180	1.217	4.96	0.758	0.062	0.253	32.75	3.950	1.552	2.40	0.716	0.357	0.492	33.55
3	G	91	5.290	1.059	4.23	0.619	0.051	0.330	29.96	4.155	1.716	2.44	0.724	0.328	0.663	41.39
3	C	91	5.545	1.500	4.04	0.830	0.065	0.497	42.96	4.645	1.979	2.67	0.800	0.461	0.706	46.63
4	B	91	6.450	1.217	5.23	0.821	0.068	0.183	31.28	4.885	1.974	2.91	0.895	0.471	0.572	43.65
4	G	91	4.675	1.111	3.56	0.725	0.057	0.209	29.06	3.245	1.355	1.89	0.577	0.253	0.481	31.57
4	C	91	5.855	1.499	4.36	0.901	0.068	0.397	41.26	4.640	1.928	2.71	0.807	0.411	0.709	44.49
5	B	123	11.006	3.632	7.37	1.562	0.144	1.496	117.64	6.409	2.988	3.42	1.146	0.648	1.122	60.96
5	G	123	9.563	3.259	6.30	1.127	0.092	1.670	109.75	5.182	2.547	2.64	0.974	0.541	1.097	57.39
5	C	123	8.542	3.255	5.29	1.107	0.087	1.781	108.38	5.742	2.858	2.88	0.990	0.689	1.117	59.66
6	B	123	11.868	4.186	7.68	1.834	0.158	1.619	133.78	6.637	3.218	3.42	1.248	0.791	0.842	62.53
6	G	123	10.291	3.331	6.96	1.321	0.119	1.460	107.64	5.327	2.580	2.75	0.908	0.519	1.141	56.69
6	C	123	10.577	3.528	7.05	1.315	0.109	1.678	118.10	5.704	3.008	2.70	0.996	0.664	1.308	63.00
7	B	124	10.041	2.976	7.07	1.597	0.149	0.895	90.24	5.634	2.558	3.08	1.066	0.625	0.799	53.00
7	G	124	9.699	3.334	6.36	1.373	0.129	1.410	106.14	5.331	2.592	2.74	0.988	0.673	0.891	52.82
7	C	124	9.703	3.433	6.27	1.362	0.127	1.559	113.02	8.037	3.891	4.15	1.479	1.019	1.479	75.65
8	B	126	9.513	2.980	6.53	1.266	0.111	1.244	94.92	5.849	2.892	2.96	1.067	0.635	1.200	63.59
8	G	126	8.339	2.812	5.53	1.176	0.109	1.180	89.46	5.101	2.522	2.58	0.875	0.668	0.964	51.38
9	G	163	9.720	3.684	6.04	1.280	0.082	1.908	116.83	10.800	5.762	5.04	1.719	1.119	2.957	182.74
9	C	163	10.420	4.258	6.16	1.455	0.076	2.141	136.92	11.400	5.922	5.48	1.951	1.131	2.755	144.88
10	B	165	11.182	3.764	7.42	1.608	0.116	2.242	118.89	8.620	4.277	4.34	1.448	0.796	1.947	99.33
10	G	165	10.210	3.216	6.99	1.536	0.116	1.377	95.22	9.615	5.135	4.48	1.631	0.785	2.732	145.83
10	C	165	11.125	4.321	6.80	1.507	0.111	2.392	141.84	9.860	5.445	4.42	1.404	0.875	3.062	153.47
11	B	195	15.040	4.966	10.07	1.904	0.165	2.423	151.70	14.010	7.034	6.98	2.397	1.461	3.127	166.95
11	G	195	11.930	4.236	7.69	1.413	0.124	2.382	133.05	12.770	7.147	5.62	1.875	0.996	4.145	207.21
11	C	195	13.210	5.597	7.61	1.493	0.134	3.499	185.94	12.350	6.568	5.78	1.936	1.271	3.284	174.67
12	B	231	16.470	6.311	10.16	2.107	0.131	3.426	200.39	10.800	5.364	5.44	1.957	1.419	2.182	113.87
12	G	231	15.704	6.562	9.14	2.003	0.123	3.809	213.99	10.327	6.041	4.29	1.777	1.042	3.335	156.20
12	C	231	14.094	6.303	7.79	1.355	0.119	4.548	242.31	9.416	5.554	3.86	1.393	0.823	3.146	153.70
13	B	285	18.686	8.240	10.45	2.212	0.185	5.030	269.83	14.132	7.791	6.34	2.669	1.543	3.444	179.52
13	C	285	12.844	5.827	7.02	1.584	0.120	3.797	194.53	12.526	7.343	5.18	1.967	1.183	3.995	199.13
14	B	330	19.911	9.844	10.07	2.934	0.209	5.989	324.90	14.514	7.967	6.55	2.627	1.455	3.362	200.96
14	G	330	16.808	7.670	9.13	1.916	0.144	5.050	259.87	12.596	7.335	5.26	1.969	1.198	3.983	202.96
14	C	330	20.432	10.100	10.33	2.130	0.169	7.159	347.94	15.515	9.377	6.14	2.352	1.742	5.034	275.74
15	B	332	25.400	13.023	12.38	2.447	0.093	9.736	455.55	16.040	8.251	7.79	2.696	1.402	3.441	198.98
15	G	332	18.050	8.752	9.30	1.941	0.151	5.808	301.07	15.730	9.219	6.51	2.421	1.558	5.163	250.91
15	C	332	22.430	14.688	7.74	1.568	0.080	12.408	531.15	15.540	9.535	6.00	2.271	1.074	5.807	281.74

APPENDIX 1.6: Distribution of dissected lean in left carcass side

Litter	Sex	Age at slaughter (days)	kg Dissected lean: hand	collar	rib back	rib streak	rump back	rump streak	ham	Total in left carcass side (kg)
1	B	52	0.616	0.732	0.550	0.332	0.428	0.180	1.050	3.888
1	G	52	0.615	0.764	0.524	0.384	0.482	0.224	1.170	4.163
1	C	52	0.558	0.764	0.578	0.378	0.438	0.178	1.038	3.932
2	B	55	0.346	0.410	0.322	0.162	0.172	0.086	0.492	1.990
2	G	55	0.402	0.540	0.386	0.260	0.276	0.102	0.788	2.754
2	C	55	0.578	0.662	0.552	0.310	0.382	0.145	1.028	3.657
3	B	91	1.446	1.372	1.126	0.618	0.802	0.396	2.092	7.852
3	G	91	1.390	1.334	1.210	0.750	0.908	0.434	2.142	8.168
3	C	91	1.190	1.394	1.260	0.676	1.034	0.482	2.142	8.178
4	B	91	1.436	1.476	1.258	0.830	0.726	0.390	2.110	8.226
4	G	91	0.916	1.058	0.666	0.464	0.532	0.274	1.530	5.440
4	C	91	1.510	1.674	1.270	0.756	0.994	0.450	2.354	9.008
5	B	123	1.564	2.178	1.512	0.676	1.278	0.612	2.748	10.568
5	G	123	1.546	1.856	1.456	0.732	1.210	0.610	3.020	10.430
5	C	123	1.652	1.738	1.326	0.773	1.018	0.564	2.782	9.853
6	B	123	2.300	2.574	1.944	1.002	2.714	0.768	3.530	14.832
6	G	123	1.524	1.636	1.428	0.548	1.264	0.528	2.664	9.592
6	C	123	1.752	2.456	1.590	0.996	1.275	0.760	3.076	11.905
7	B	124	2.028	2.300	1.652	0.758	1.252	0.584	3.055	11.629
7	G	124	1.596	1.706	1.666	1.028	1.172	0.600	2.708	10.476
7	C	124	1.762	0.954	1.530	0.956	1.384	0.470	3.064	10.120
8	B	126	1.704	2.022	1.352	0.776	1.264	0.688	3.082	10.888
8	G	126	2.002	1.990	1.826	0.785	1.356	0.666	3.070	11.695
9	G	163	2.520	3.188	2.500	1.106	2.234	1.272	4.415	17.235
9	C	163	2.248	3.270	2.616	1.094	2.158	0.450	4.368	16.204
10	B	165	2.926	4.072	2.534	2.010	1.852	1.180	4.732	19.306
10	G	165	2.592	2.963	2.848	1.640	2.230	1.146	4.497	17.916
10	C	165	2.126	3.180	2.670	1.670	1.942	1.115	4.396	17.099
11	B	195	3.348	5.215	4.657	2.173	3.238	1.676	6.642	26.949
11	G	195	3.264	4.298	3.376	1.448	3.280	1.774	5.526	22.966
11	C	195	3.826	4.112	4.122	1.790	3.080	1.636	6.156	24.772
12	B	231	3.318	5.164	3.896	1.508	2.704	1.266	6.082	23.938
12	G	231	3.724	3.932	2.778	2.184	2.722	1.460	4.828	21.628
12	C	231	2.232	3.052	2.056	1.310	2.098	0.826	4.518	16.092
13	B	285	3.780	5.976	4.222	2.586	3.012	1.876	7.234	28.686
13	C	285	2.682	4.386	3.088	2.024	3.046	1.410	6.086	22.722
14	B	330	4.602	7.358	4.282	3.148	3.736	1.832	7.714	32.672
14	G	330	3.392	5.125	4.080	2.394	3.658	2.045	6.964	27.658
14	C	330	4.546	6.068	3.684	2.798	3.558	1.788	7.120	29.562
15	B	332	4.610	6.360	4.628	2.788	3.661	1.664	7.598	31.309
15	G	332	4.640	7.032	4.501	2.670	5.191	1.640	7.382	33.056
15	C	332	3.672	5.520	3.473	2.426	2.918	1.556	6.694	26.259



APPENDIX 1.7: Change in live weight over time by an individual entire male pig from 21 to 332 days of age. The solid line delineates change in live weight according to the Gompertz function:

$$W_t = A.e^{-e^{-B(t-t^*)}}$$ where 'A' is 250 kg LW

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Growth of body components in young weaned pigs

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SUMMARY

Four experiments with 133 piglets of between 21 and 55 days of age were used to examine, by slaughter and chemical analysis, the composition of the body of young pigs. Following removal from the sow, the lipid content of the empty body decreased from about 15 to 7·6%, and in the subsequent 4 weeks had recovered only slightly to between 7·7 and 10·9%; with the exception of pigs with a particularly high intake of energy whose 42-day lipid content had increased to 13·2%. Where Y_3 was the lipid gain, X_1 the digestible energy intake (MJ) and X_2 the ratio of digestible energy to digestible crude protein (g), over all experiments $Y_3 = 7{\cdot}83X_1 + 4945X_2 - 1260$. There was little change in the protein content of pigs consequent upon the effects of either removal from the sow, pig age, diet type or nutrient intake. Over all experiments and slaughter weights; $P = 0{\cdot}164W - 100$, where P was the protein content of the body (g) and W the empty body weight (g). The efficiencies of conversion of digestible energy to energy gain in body protein and lipid were 0·36 and 0·33 respectively, associated with a constant (daily maintenance) term of 0·462 MJ ME/kg $LW^{0{\cdot}75}$. The low value for lipid is as would be expected for animals catabolizing lipid within the experimental period.

INTRODUCTION

Removal of pigs from a suckled sow, with associated changes in diet composition and nutrient supply, interrupts the pattern of liveweight growth and alters the composition of liveweight gain (Baur & Filer, 1959; Willye *et al.* 1969). For the purpose of growth studies, this intervening period between weaning and the reattainment of normal growth represents a time of confusion which nevertheless is an integral part of the normal growth pattern of pigs reared for the commercial production of meat. Changes in body composition after weaning are additionally of retrospective importance for the correct interpretation of nutrition, growth and genetic experiments which begin at or soon after the pigs are removed from the sow.

In the course of four nutrition experiments completed at Edinburgh between 1972 and 1976, 133 baby pigs were slaughtered and the chemical compositions of the empty body determined. The objectives of these experiments were respectively: to compare the growth of Hampshire and Saddleback pigs (Expt 1, Whittemore & Illius, 1974); to compare the nutritive value of cooked potato flake with maize meal (Expt 2, Whittemore, Taylor & Crooks, 1974); and to compare the nutritive value of white fish meal with dried microbial cells at a high (Expt 3) and a low (Expt 4) level of inclusion (Whittemore, Moffat & Taylor, 1976). Data collected during the course of these experiments are used here in combination and by comparison to study the growth of young pigs after weaning.

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MATERIALS AND METHODS

Full details of experimental procedures may be found in the respective reports cited above. A summary is given in Table 1, and the means and standard deviations for the data are presented in Table 2. During each experiment the pigs were housed in individual wire mesh pens fitted with nipple drinkers and were provided with feed troughs designed to minimize spillage. Empty body weight (EBW) was determined after removal of intestinal contents at slaughter. The entire empty bodies were frozen and then minced twice through 13 and 6 mm plates and once through a 3 mm

Table 1. *Summary of experimental details*

Experiment	Diet*	Breed†	Age at slaughter	Age weaned	Diet composition		Number of pigs
					MJ DE/kg D.M.	g DCP/kg D.M.	
1	—	H	28	28	Suckled by sow‡		8
	—	S	28	28	Suckled by sow		8
	DSM§	H	55	28	19·9	297	9
	DSM	S	55	28	19·9	297	9
2	—	LWL	21	21	Suckled by sow		13
	CPF‖	LWL	53	21	16·2	168	9
	M¶	LWL	53	21	15·3	174	9
3	—	LWL	21	14	15·5	217	19
	DMC**	LWL	42	14	15·6	219	15
	WFM††	LWL	42	14	15·4	214	15
4	DMC‡‡	LWL	42	14	15·8	176	9
	WFM§§	LWL	42	14	15·6	162	10

* All diets were supplemented with vitamins, minerals, trace elements and an antibiotic.
† H, Hampshire; S, Saddleback; LWL, Large White × Landrace.
‡ Piglets were also offered a supplementary 'creep-feed'.
§ 50 % dried skimmed milk, 10 % dried whole milk, 13 % herring meal, 13 % oat flakes, 5 % fat, 5 % sucrose, 3 % glucose.
‖ 78 % cooked potato flake, 10 % soya-bean meal, 10 % white fish meal.
¶ 78 % maize meal, 10 % soya-bean meal, 10 % white fish meal.
** 20 % dried microbial cells, 20 % whey, 30 % maize, 10 % wheat, 17·5 % barley.
†† 20 % white fish meal, 20 % whey, 30 % maize, 10 % wheat, 17·5 % barley.
‡‡ 10 % dried microbial cells, 20 % whey, 30 % maize, 20 % wheat, 17·5 % barley.
§§ 10 % white fish meal, 20 % whey, 30 % maize, 20 % wheat, 17·5 % barley.

plate. Dry matter was determined by oven-drying fresh mince at 95 °C to constant weight. Samples for chemical analysis were freeze-dried and then milled. Gross energy (GE) was measured by adiabatic bomb, nitrogen by Kjeldahl digestion and lipid by use of the equation; lipid = (GE − 0·1475 N)/0·0393, which assumes the energy content of protein and lipid to be 23·6 and 39·3 MJ/kg respectively. Chemical compositions of the pigs slaughtered at the start of each experiment were used to predict the initial composition of the remaining pigs grown to final weight. Linear regression analysis was used to describe the relationship between the weight of body components and the weight of the empty body, and between the lipid and protein composition of the gain and digestible energy (DE) and digestible crude protein (DCP) intake. Curvilinear regression and logarithmic transformations were also fitted, but in no case was there a significant improvement in explanation of the variance.

RESULTS

Growth patterns

There were differences between the four experiments in the pattern of live-weight gain (Fig. 1). In Expts 1 and 2, in which weight recording began on the day of weaning (at 28 and 21 days of age, respectively), no live-weight growth was made during the following 7 days and pigs consumed little feed (between 50 and 200 g daily). In the cases of Expts 3 and 4 the pigs were weaned at 14 days of age, 7 days before the live weight of the pigs began to be recorded at 21 days of age, and in these last two experiments effective weight gains were achieved between 3 and 4 weeks of age. It is apparent from Fig. 1 that although growth is markedly interrupted during the week following weaning, normal growth can be soon reattained (after 35 days of age in the case of Expts 1 and 2).

Daily nutrient intakes expressed per kg EBW (Table 2) suggest that pigs in Expts 3 and 4 were better nourished than those in Expt 2, with Expt 1 intermediate. Energy:protein ratio expressed as DE:DCP was higher for Expts 2 and 4 (0·092 and 0·093 respectively) than for Expts 1 and 3 (0·067 and 0·071 respectively).

Body composition

Suckling pigs slaughtered at 28 and 21 days of age on the day of weaning (Expts 1 and 2) had similar percentage compositions despite differences in age and breed (Fig. 2). Pigs weaned at 14 days of age but not slaughtered until 21 days of age (Expt 3) contained only half the percentage of

Table 2. *Means and standard deviations for data used in analyses*

Experiment	Age (days)	Duration of trial (days)	Number of pigs	Empty body weight (g)	Chemical content of the empty body					Nutrient intake			
					Water (g)	GE (MJ)	Lipid (g)	Protein (g)	Ash (g)	DCP (g)	DE (MJ)	g DCP/day/kg EBW	MJ DE/day/kg EBW
1	28		16	6597 ± 1824	4402 ± 1162	62 ± 20	1005 ± 353	966 ± 284	193 ± 50	—	—	—	—
	55	27	18	14711 ± 2543	10346 ± 1634	115 ± 30	1504 ± 561	2368 ± 390	421 ± 65	2673 ± 414	179 ± 28	9·4 ± 0·77	0·63 ± 0·051
2	21		13	5525 ± 903	3751 ± 589	51 ± 10	815 ± 171	792 ± 140	142 ± 23	—	—	—	—
	53	32	18	11508 ± 1463	8177 ± 973	89 ± 15	1255 ± 269	1679 ± 264	361 ± 58	1821 ± 288	168 ± 26	6·6 ± 0·86	0·61 ± 0·072
3	21		19	4545 ± 1076	3340 ± 709	30 ± 10	346 ± 162	677 ± 164	142 ± 36	—	—	—	—
	42	21	30	11611 ± 1708	8439 ± 1144	79 ± 17	896 ± 251	1856 ± 309	380 ± 85	2491 ± 491	176 ± 35	13·9 ± 1·97	0·99 ± 0·139
4	42	21	19	10039 ± 904	6768 ± 598	86 ± 9	1330 ± 133	1517 ± 196	299 ± 31	2236 ± 198	208 ± 17	14·3 ± 1·41	1·33 ± 0·141

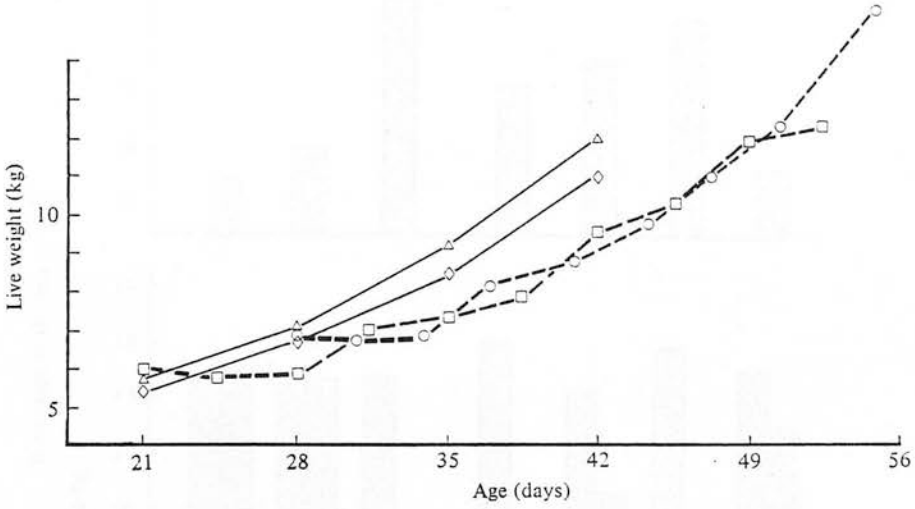

Fig. 1. Live-weight growth of pigs. ○- - -○, Expt 1 (weaned at 28 days); □- - -□, Expt 2 (weaned at 21 days); △—△, Expt 3 (weaned at 14 days); ◇—◇, Expt 4 (weaned at 14 days).

lipid of unweaned pigs of the same age. Lipid loss was not however balanced by an equivalent increase in the percentage of protein, such as might have been expected if the loss of body lipid had been accompanied by an equal loss of body mass; thus the water:protein ratio in the empty body of 21-day old pigs was 4·75 in Expt 2 and 4·93 in Expt 3. It is evident from Fig. 2 that the percentage of protein in the body was a relatively intransigent character, varying only from 14·3 to 16·1% over all slaughter weights and nutritional regimes. Conversely, the percentage of lipid in the body varied from 7·6 to 15·2%.

At the termination of Expts 1 and 2 (at 55 and 53 days) the pigs contained a lower percentage of lipid than at the beginning (28 and 21 days), whereas for Expt 3 the percentage of lipid at 42 days was similar to that at 21 days of age. In Expt 4 the percentage of lipid at 42 days was almost twice that which it had been 3 weeks earlier.

Linear regression relationships between the body components (Y) and EBW (X) are presented in Table 3. In general, correlation coefficients between the body components and EBW were high; the exceptions being ash, and lipid in the case of Expt 4 (water, $r = 0{\cdot}95-0{\cdot}99$; protein, $r = 0{\cdot}87-0{\cdot}99$; lipid, $r = 0{\cdot}87-0{\cdot}92$ (Expt 4, $r = 0{\cdot}62$); ash, $r = 0{\cdot}56-0{\cdot}92$; gross energy, $r = 0{\cdot}94-0{\cdot}98$). Table 3, together with Figs 3 and 4, demonstrates the comparative constancy of the protein content of the empty body in contrast to the variability of the lipid content. In the case of the lipid composition (Fig. 4), a comparison of suckled pigs (Expts 1 and 2 at 28 and 21 days) with those weaned (all others) would suggest that the effect of weaning was to shift the regression line downwards. Weaning, age and diet appear to have had relatively little effect upon the relationship between protein content and empty body weight.

Composition of gain

Empty-body-weight gain and the composition of the gain varied between experiments (Tables 4, 5, and Fig. 5). Protein gains were at least twice the lipid gains for Expts 1, 2 and 3, while for Expt 4 protein gains were slightly less than lipid gains. Table 5 shows that the daily gain of protein per kg EBW was rather lower for Expt 2 than for the other experiments, while the gains of lipid were very much higher in Expt 4. In this respect, Table 2 indicates that the daily intake of DCP/kg EBW was lowest for Expt 2, while the daily intake of DE/kg EBW was highest for Expt 4.

Linear regression equations describing the relationship between the chemical composition of the gain and the gain in EBW of the pigs are presented in Table 6. For Expts 1 and 2, the slopes for lipid are higher than those for protein; which is apparently contradictory to the expectation that one might have formed following perusal of Table 5 and Fig. 5. Similarly, the expectation of a steeper slope for lipid than for protein in Expt 4 was not fulfilled.

Relationship to nutrient intake

Table 7 gives the single regression relationships for the combined data from all experiments and

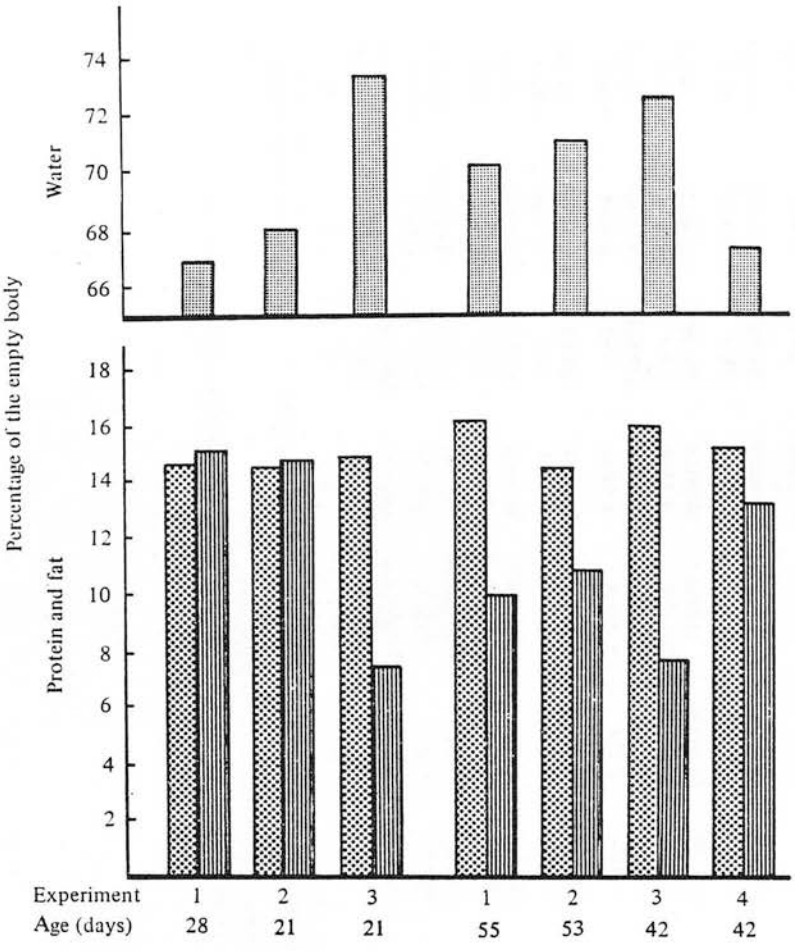

Fig. 2. Percentage composition of pigs. ▦, protein; ▥, fat; ▩, water.

suggests that 1 g increment of DCP was associated with 2·5 g of EBW gain, 0·49 g of protein gain and 0·28 g of lipid gain; while 1 MJ increment of DE was associated with 22 g of EBW gain, 3·3 g protein gain and 8·2 g of lipid gain. Intake of DCP accounted for about half the variance in protein gain while DE intake accounted for about two-thirds of the lipid gain. The nutrient intakes of the pigs can be defined by expression of DE intake (X_1) and the DE:DCP ratio (X_2). Where Y_1 is the EBW gain, Y_2 protein gain and Y_3 lipid gain, the following multiple regression relationships relate to the combined data from all experiments:

$$Y_1 = 27{\cdot}7\ (\pm 3{\cdot}87)\ X_1 - 81\,814\ (\pm 10\,000)\ X_2 + 7782\ (\pm 973)\ (r = 0{\cdot}74), \quad (1)$$

$$Y_2 = 4{\cdot}57\ (\pm 0{\cdot}778)\ X_1 - 18\,524\ (\pm 2021)\ X_2 + 1679\ (\pm 196)\ (r = 0{\cdot}75), \quad (2)$$

$$Y_3 = 7{\cdot}83\ (\pm 0{\cdot}625)\ X_1 + 4945\ (\pm 1623)\ X_2 - 1260\ (\pm 157)\ (r = 0{\cdot}83). \quad (3)$$

The relationship between energy:protein ratio in the gain and DE:DCP ratio in the diet was rather poor. Figure 6 indicates there to have been a wide range of energy:protein ratios in the gain at each dietary DE:DCP ratio, and a resolute failure by pigs on Expt 2 to show a high energy:protein ratio in the gain despite a high DE:DCP ratio in the diet. The relationship is confounded with the effects of feed intake; pigs on Expt 2 ingested only half the nutrients per kg EBW as did pigs on Expt 4 fed a diet of similar DE:DCP ratio (Table 2). Intakes of DCP were similar for Expts 3 and 4, but the DE:DCP ratio differed widely; use of these data yield the relationship

$$Y_4 = 1{\cdot}39\ (\pm 0{\cdot}115)\ X_2 - 0{\cdot}06\ (\pm 0{\cdot}009)\ (r = 0{\cdot}87), \quad (4)$$

where Y_4 is the energy:protein ratio in the gain and X_2 the DE:DCP ratio in the diet.

The relationship between daily DE intake/kg

Table 3. *Linear regression of chemical composition of piglets (Y) on empty body weight at slaughter (X), $Y = a + bX$ (the standard error is given in parentheses)*

Experiment	Age (days)	Water (g)		Protein (g)		Lipid (g)		Ash (g)		Gross energy (MJ)	
		b	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*
1	28	0·632	231·0	0·153	−40·0	0·171	−120·7	0·0239	35·7	0·0103	−5·69
		(0·0212)	(144·44)	(0·0082)	(55·95)	(0·0245)	(167·15)	(0·0036)	(24·46)	(0·0009)	(6·24)
	55	0·635	1004·4	0·140	308·2	0·196	−1377·8	0·0168	173·8	0·0110	−46·9
		(0·0242)	(360·33)	(0·0156)	(232·88)	(0·0253)	(376·99)	(0·0048)	(71·02)	(0·00096)	(14·39)
2	21	0·647	176·9	0·151	−45·1	0·172	−136·4	0·0202	30·4	0·0103	−6·41
		(0·0248)	(138·55)	(0·0100)	(56·50)	(0·0240)	(134·26)	(0·0045)	(25·16)	(0·0010)	(5·53)
	53	0·660	580·1	0·156	−119·9	0·160	−586·6	0·0301	14·9	0·0100	−25·9
		(0·0200)	(231·32)	(0·0226)	(261·97)	(0·0226)	(261·79)	(0·0065)	(74·94)	(0·0008)	(9·15)
3	21	0·656	359·8	0·151	−6·85	0·136	−271·4	0·0307	2·85	0·0089	−10·8
		(0·0158)	(73·74)	(0·0053)	(24·50)	(0·0159)	(73·99)	(0·0032)	(15·03)	(0·0006)	(2·84)
	42	0·665	719·7	0·175	−177·0	0·135	−676·8	0·0279	55·3	0·0095	−30·8
		(0·0149)	(174·95)	(0·0089)	(104·59)	(0·0110)	(126·01)	(0·0078)	(91·56)	(0·0004)	(4·70)
4	42	0·655	193·1	0·201	−497·3	0·0915	411·1	0·0253	45·5	0·0069	16·5
		(0·0220)	(222·98)	(0·0200)	(199·99)	(0·0279)	(281·21)	(0·0058)	(58·56)	(0·0018)	(18·57)
All	39	0·706	−9·24	0·164	−100·2	0·097	88·9	0·0299	7·46	0·0077	1·03
		(0·0061)	(62·69)	(0·0026)	(26·35)	(0·0068)	(69·42)	(0·0011)	(11·53)	(0·00024)	(2·51)

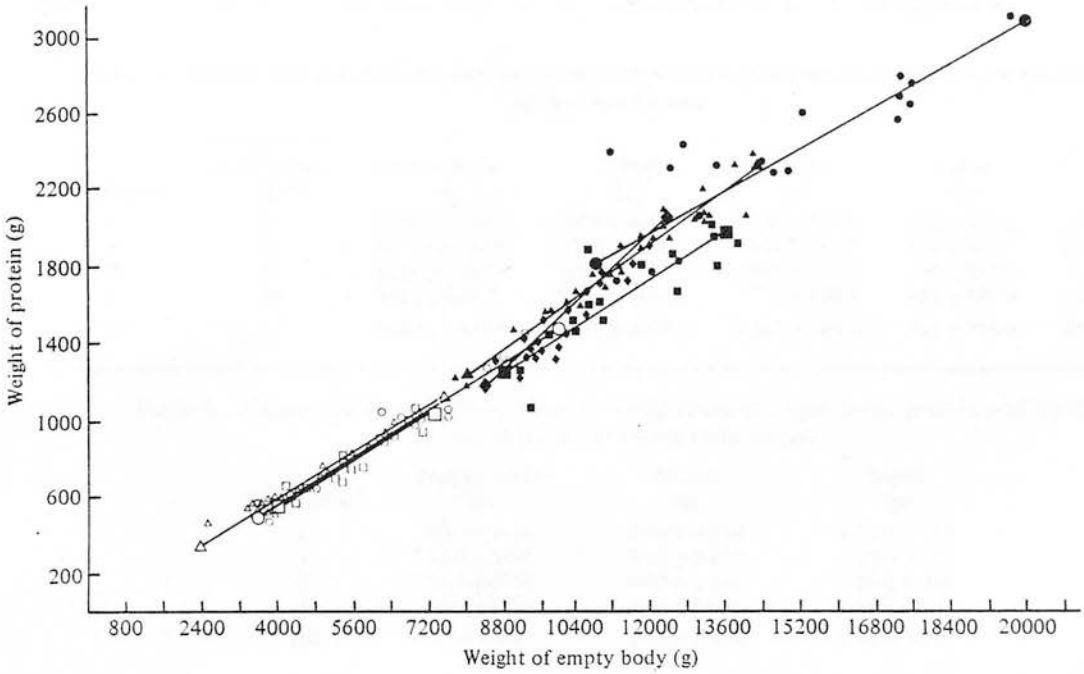

Fig. 3. Protein content of the empty body of pigs. ○, Expt 1 (28 days, at weaning); □, Expt 2 (21 days, at weaning); △, Expt 3 (21 days, 7 days post weaning); ●, Expt 1 (55 days); ■, Expt 2 (53 days); ▲, Expt 3 (42 days); ◆, Expt 4 (42 days).

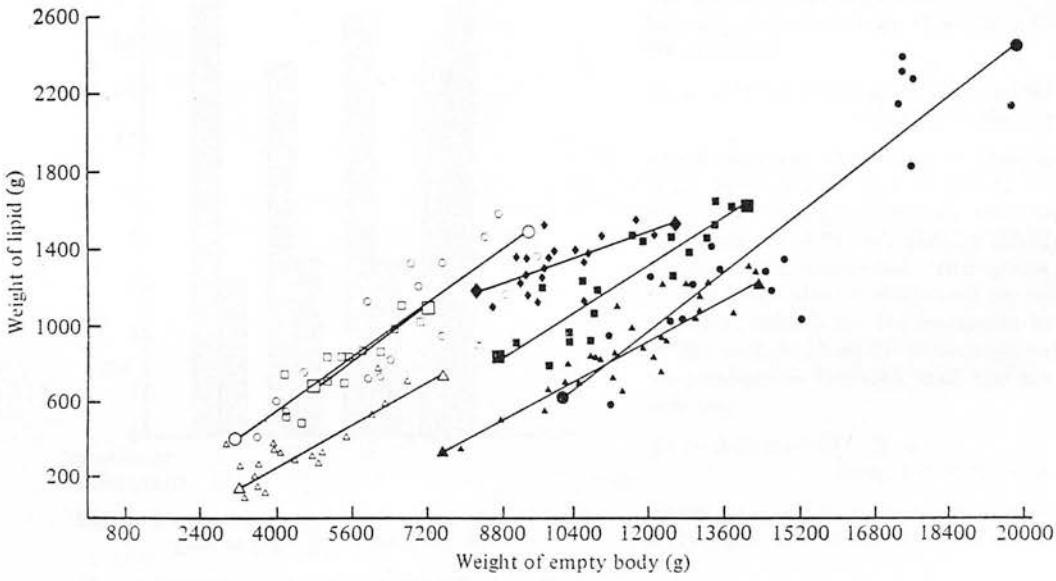

Fig. 4. Lipid content of the empty body of pigs. ○, Expt 1 (28 days, at weaning); □, Expt 2 (21 days, at weaning); △, Expt 3 (21 days, 7 days post weaning); ●, Expt 1 (55 days); ■, Expt 2 (53 days); ▲, Expt 3 (42 days); ◆, Expt 4 (42 days).

Table 4. *Means and standard deviations for the components of the empty-body gain for the duration of the experiments*

Experiment	Duration of experiment (days)	Empty body (g)	Water (g)	Protein (g)	Lipid (g)	Ash (g)
1	27	8226 ± 1186·6	6008 ± 830·9	1436 ± 215·6	522 ± 357·4	229 ± 50·4
2	32	5873 ± 1181·6	4344 ± 799·4	871 ± 194·7	419 ± 243·7	217 ± 53·6
3	21	6234 ± 1487·8	4558 ± 1019·2	1061 ± 291·1	436 ± 214·9	212 ± 77·9
4	21	5114 ± 630·2	3182 ± 418·9	779 ± 136·9	930 ± 137·3	145 ± 25·5
All	—	6330 ± 1602·9	4512 ± 1245·7	1037 ± 324·8	561 ± 314·8	202 ± 65·6

Table 5. *Means and standard deviations for daily gains of empty body, protein and lipid, expressed per kg of empty-body weight*

Experiment	Empty body (g)	Protein (g)	Lipid (g)
1	29·0 ± 2·14	5·09 ± 0·759	1·72 ± 1·013
2	21·3 ± 2·96	3·14 ± 0·472	1·50 ± 0·818
3	34·7 ± 5·83	5·88 ± 1·186	2·36 ± 1·030
4	32·7 ± 3·81	4·95 ± 0·635	5·98 ± 1·086
All	30·2 ± 6·57	4·93 ± 1·320	2·85 ± 1·981

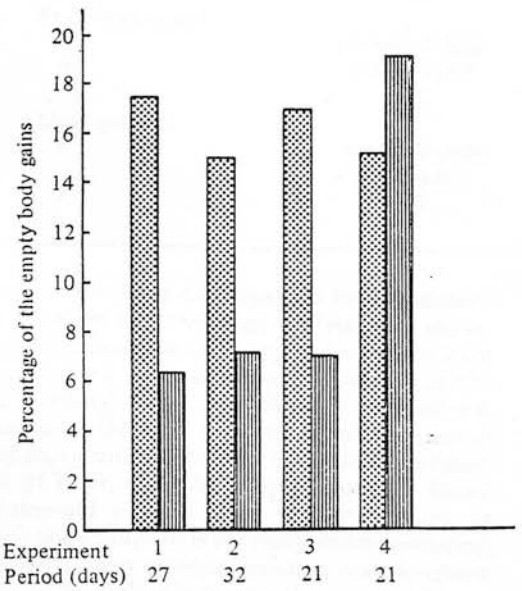

Fig. 5. Percentage composition of the empty-body gain of pigs. ▦, protein; ▥, fat.

EBW (E_I) and the daily energy gained/kg EBW (E_R) is shown in Fig. 7 and can be described as

$$E_I = 2{\cdot}99\ (\pm 0{\cdot}193)\ E_R + 0{\cdot}238\ (\pm 0{\cdot}0464)\ (r = 0{\cdot}86). \quad (5)$$

The relationship suggests digestible energy to have been converted into energy gain with an efficiency of 0·33, and that at zero energy retention there was an associated intake of 0·238 MJ DE/kg EBW/day. Multiple regression of DE intake upon energy gain divided into lipid energy (E_L) (39·3 MJ/kg) and protein energy (E_P) (23·6 MJ/kg) yielded the equation

$$E_I = 2{\cdot}98\ (\pm 0{\cdot}219)\ E_L + 2{\cdot}44\ (\pm 0{\cdot}548)\ E_P + 0{\cdot}292\ (\pm 0{\cdot}0651)\ (r = 0{\cdot}86) \quad (6)$$

which suggests efficiencies of conversion of DE to body lipid of 0·34 and of DE to body protein of 0·41. Zero energy retention was associated with an intake of 0·292 MJ DE/kg EBW/day. Energy expenditures associated with gains of lipid and protein may also be estimated by subtraction of a constant term 0·238 MJ (equation 5) from the DE intake and dividing the remaining energy available for production between lipid and protein gains; in this way

$$E_I = 3{\cdot}01\ (\pm 0{\cdot}216)\ E_L + 2{\cdot}85\ (\pm 0{\cdot}245)\ E_P\ (r = 0{\cdot}98), \quad (7)$$

which suggests efficiencies of conversion of DE to body lipid of 0·33 and of DE to body protein of 0·36.

DISCUSSION

The interruption to live-weight growth which can occur following weaning, and which is often evidenced by no weight change, appears not to be the symptom of stasis, but of lipid loss. The reduction in percentage lipid in the empty body of weaned pigs compared with those suckling did not

Table 6. *Linear regression of chemical composition of the gain of pigs (Y) on empty-body weight gain (X)* $Y = a + bX$ *(the standard error is given in parentheses)*

	Water		Protein		Lipid		Ash	
Experiment	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*
1	0·670	499	0·124	418	0·204	−1158	0·010	147
	(0·0509)	(423·0)	(0·0332)	(275·8)	(0·0554)	(459·8)	(0·0103)	(85·8)
2	0·667	436	0·124	144	0·172	−589	0·032	31·9
	(0·0241)	(143·9)	(0·0269)	(160·8)	(0·0280)	(167·6)	(0·0081)	(48·25)
3	0·679	322	0·186	−96·8	0·129	−369	0·023	67·4
	(0·0166)	(106·3)	(0·0116)	(74·34)	(0·0123)	(78·5)	(0·0089)	(56·78)
4	0·652	−150	0·165	−63·4	0·128	278	0·022	34·0
	(0·0318)	(163·7)	(0·0343)	(176·4)	(0·0429)	(220·7)	(0·0083)	(42·53)

Table 7. *Linear regression of chemical composition of the gain of pigs (Y) on intake of nutrients (X),* $Y = a + bX$. *Values relate to the combined data from Experiments* 1, 2, 3 *and* 4

	Independent variable (*X*)		
Dependent variable (*Y*)	DCP intake (g)	DE intake (MJ)	DE:DCP
EBW gain (g)			
b	2·52 ± 0·234	21·9 ± 5·09	−68567 ± 12527
a	454 ± 558·0	2332 ± 940·2	11785 ± 1008
r	0·76	0·43	0·52
Protein gain (g)			
b	0·490 ± 0·0501	3·27 ± 1·082	−16372 ± 2354
a	−104 ± 119·3	441 ± 200·1	2339 ± 189·4
r	0·73	0·32	0·61
Lipid gain (g)			
b	0·282 ± 0·0642	8·18 ± 0·644	8637 ± 2609
a	−96·3 ± 152·7	−929 ± 119·1	−126 ± 218
r	0·43	0·81	0·33

appear to have been accompanied by a commensurate increase in percentage protein; the movement of lipid from the body appears rather to have been associated with an influx of water. If the finding of Elsley (1965), and others, is accepted and it is assumed that the percentage composition of suckled pigs is unlikely to alter appreciably between 14 and 21 days, then the body proportions found for 21-day-old pigs on Expt 2 may be used to calculate the change in body composition occurring during the 7 days between weaning and slaughter on Expt 3. By such calculations the pigs could have lost some 324 g lipid and gained some 254 g water and 25 g protein. Comparison of Figs 3 and 4 serves to demonstrate that the percentage of protein in the empty body is little influenced by events which have the most dramatic negative effects upon the percentage of body lipid. In general, the percentage of protein in the empty body of 5–15 kg piglets appears largely unrelated to dietary treatment, unaffected by weaning and independent of the percentage of lipid. In contrast, percentage lipid is dramatically reduced after weaning; its rate of recovery being influenced by the subsequent pattern of ingestion of nutrients. Only in the case of Expt 4 was the percentage of lipid in the body of weaned pigs at 42 days approaching that of the suckling pigs; these pigs had ingested by far the greatest amount of energy.

Consequent upon the phase of lipid catabolism, measurements of net tissue gains of lipid almost certainly underestimate the true rates of lipid anabolism. Thus Fig. 5 appears to present evidence favouring a slightly different interpretation than that indicated by Table 6, but the data are compatible if the perfectly reasonable assumption is made that during the early part of the experimental period the pigs lost lipid but not protein, while subsequent growth comprised both tissues. Precisely this pattern of tissue loss and regrowth has recently been demonstrated in young pigs given restricted feed and then realimented (Tullis

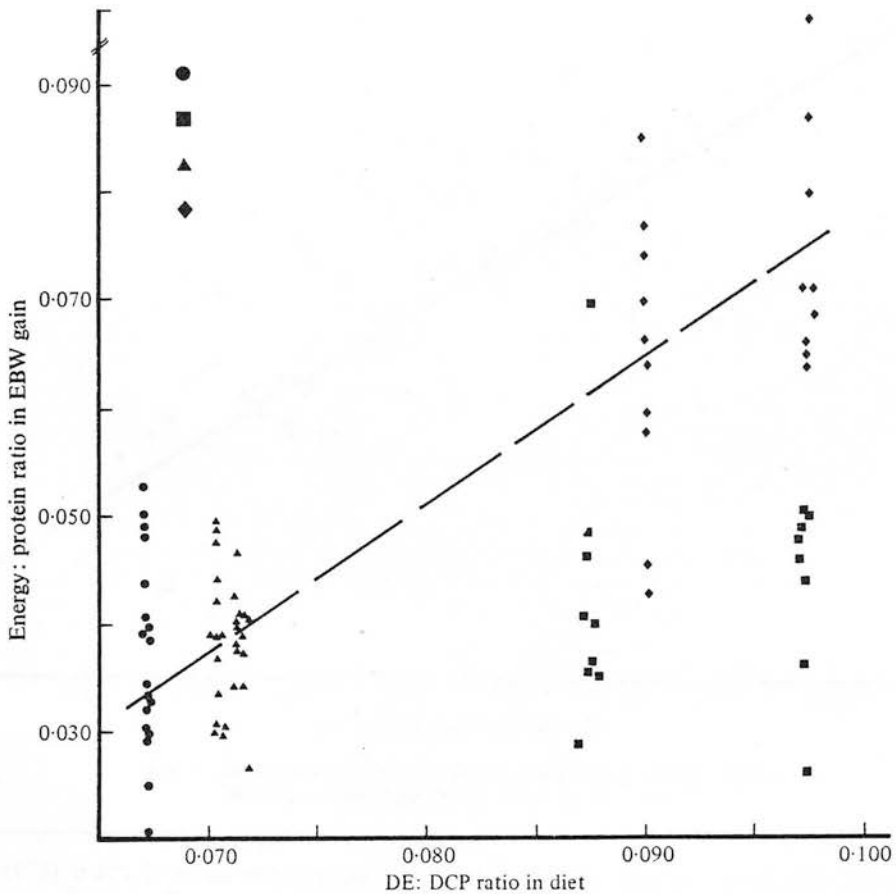

Fig. 6. Relationship between energy protein ratios in diet and empty-body weight gain. ●, Expt 1; ■, Expt 2; ▲, Expt 3; ◆, Expt 4. The broken line refers to Expt 3 and Expt 4 only.

& Whittemore, 1978). For Expts 1 and 2 fat was a greater proportion of the gain than protein (Table 6), 6), while for Expts 3 and 4 the reverse was the case; this may have been related to the measurements made upon the latter pigs commencing 7 days after weaning and therefore including a lower proportion of the total lipid losses within the experimental period.

There was a positive relationship between energy intake and rate of lipid gain (Tables 2, 5 and 7). It was particularly evident that pigs consuming most energy made the best lipid gains (Expt 4), while in the case of Expt 2 it appeared that a shortage of dietary protein might have been the cause of a reduction in the rate of protein gain.

Energy intake associated with zero energy retention was estimated to be 0·238 or 0·292 MJ DE/kg EBW/day depending upon method of calculation (extrapolation or multiple regression). The average empty-body weight of the pigs during the growth periods studied was 8·7 kg, or if EBW = 0·94 live weight, 5·3 kg $LW^{0.75}$. If it is assumed that ME = 0·96 DE, then energy intake as zero retention may be calculated to be 0·375 or 0·462 MJ ME/kg $LW^{0.75}$/day. The higher value is more in accord with other published estimates for the maintenance requirement of pigs, although both values are within the range recorded in the literature; for example, 0·365–0·385 (Holmes, 1973), 0·418 (Verstegen *et al.* 1973), 0·455–0·570 (Sharma, Young & Smith, 1971), 0·524 (Jordan, 1974). The estimate of the efficiency of utilization of DE for protein gain of 0·41 (0·39 ME) by multiple regression is a little lower, but similar, to some other reported values (Kotarbińska (1969), 0·35; Close, Verstegen & Mount (1973), 0·58; Thorbek (1975), 0·48). The estimate of the efficiency of utilization of DE for lipid gain of 0·34 (0·33 ME) is however much lower than the published range (for example; Kotarbińska (1969), 0·73; Close *et al.* (1973), 0·70;

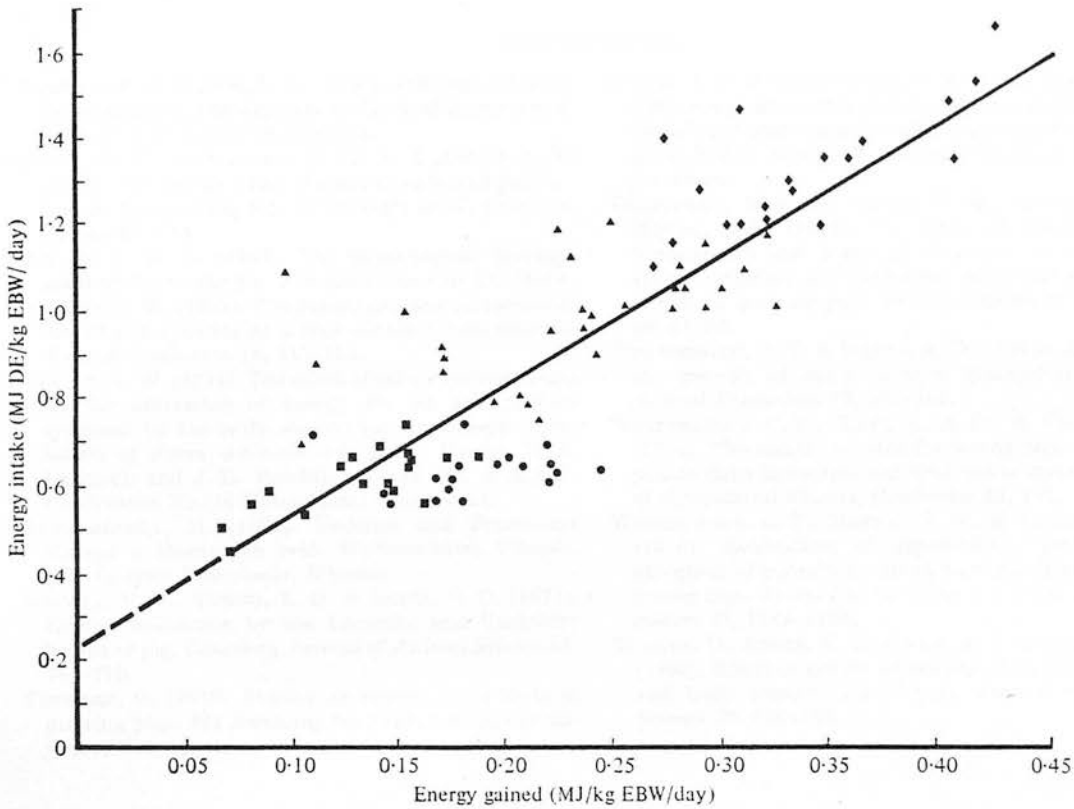

Fig. 7. Relationship between energy gained and energy intake.
●, Expt 1; ■, Expt 2; ▲, Expt 3; ◆, Expt 4.

Thorbek (1975), 0·77). It would thus appear that it is the estimate for the efficiency of the utilization of DE for lipid gain which is particularly depressed. This finding is entirely consistent with the suggestions that there was a phase of lipid catabolism during the period of measurement of tissue gains and that the actual amount of lipid gain upon which energy was expended was greater than what the difference between initial and final compositions would suggest.

A general conclusion from the data might be as follows. After weaning, pigs suffer from a transient nutrient shortage which interrupts growth. During this time, although live weight may remain static, lipid is catabolized and water retention is enhanced. The proportion of the body which is protein does not greatly change, while the lipid proportion is reduced and the water content increased. Subsequent gains of both protein and lipid, particularly the latter, are influenced by the nutrient intake and the dietary DE:DCP ratio.

Further investigations are currently in progress to determine in detail the nature of the changes which take place in a young pig's body during lipid depletion and the importance of these changes to the subsequent pattern of growth.

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CHEMICAL AND DISSECTED COMPOSITION CHANGES IN WEANED PIGLETS

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ABSTRACT

Twenty-four pigs were weaned at 21 days of age and given restricted feed allowances for the subsequent 8 days. Eight suckled pigs served as control and gained 320 g daily, of which approximately 40 g were lipid and 40 g protein. Pigs were slaughtered at 2-day intervals, physically dissected into non-carcass, carcass fatty tissue and carcass muscle plus bone, and these fractions were then analysed for water, protein and lipid. On average, weaned pigs made small positive body-weight gains. In comparison with suckled pigs, weaned pigs contained more water and less lipid but the same protein, and more non-carcass and less carcass fatty tissue but similar carcass muscle plus bone. Losses of lipid were offset by gains of water and associated with an increase in the percentage water content of carcass fatty tissue. At zero weight gain, pigs lost 43 g carcass fatty tissue, gained 37 g non-carcass, lost 56 g lipid and gained 53 g water, while carcass muscle plus bone and protein gains were themselves not significantly different from zero. No change in carcass fatty tissue weight was associated with counterbalancing losses of lipid (18 g) and gains of water (15 g) and protein (3 g). Lipid catabolism to support anabolism of essential body tissues commenced in the weaned pigs when weight gains fell below 193 g/day; this was about two-thirds of the gains achieved by the suckled control pigs. Plasma free fatty acid concentrations indicated that maximum lipid catabolism to occur on the 2nd day after weaning, and to reduce thereafter as body fat stores were progressively depleted.

INTRODUCTION

FOLLOWING weaning, piglets usually suffer a growth check associated with a temporary reduction in voluntary feed intake. Previous observations summarized by Whittemore, Aumaitre and Williams (1978) indicated that pigs usually make no live-weight change or experience a slight live-weight loss in the week after weaning. Under good management, linear growth recommences thereafter. There is no doubt that concomitant with the growth check is a loss of lipid (Whittemore *et al.*, 1978), but the nature of the changes in the composition of the body during this time are not adequately quantified. It appears that animals can lose proportionately more lipid that live weight, whereas changes in the proportions of protein and water are speculative, as are the sites in which compositional changes occur.

The contribution of live-weight loss to the energy economy of animals is an important unknown in the estimation of energy requirement. It is an essential first step to analyse the composition of the live-weight change, and to check the validity of simplistic assumptions; for example, that live-weight stasis implies body composition stasis, that live-weight loss is a reversal of live-weight gain, or that live-weight loss is a direct measure of lipid catabolism.

Pigs are born with little fat, make rapid fat gains in the first 3 weeks of life, but thereafter, if unweaned, growth has a relatively constant composition (Widdowson, 1950; Manners and McCrea, 1963; Wood and Groves, 1965). Elsley (1965) determined the percentages of water, protein, and fat in the body to be respectively: 81·5, 11·0, 1·4 at birth; 68·6, 14·4, 14·2 at 21 days; and 67·8, 14·6, 14·6 at 56 days of age. When fat is lost from the body, the proportion of body water increased (Widdowson and McCance, 1955). Such an increase would follow from a higher proportion of lean tissue which is naturally some seven times wetter than fatty tissue. The possibility of water invasion such as to increase the water:protein ratio has been

proposed (Whittemore *et al.*, 1978), but the tissue carrying this extra water was not defined.

MATERIAL AND METHODS

Thirty-two Large White × Landrace pigs of 6·09 (s.e. 0·14)kg live weight from eight litters were weighed and allocated in pairs at 21 days of age to one of 16 treatments involving four levels of feeding (weaned and offered 50 g, 100 g, or 200 g of diet once daily; or unweaned, suckled by their dam), and four times of slaughter (2, 4, 6 or 8 days after allocation). Weaned pigs were housed in individual wire-mesh cages at an ambient temperature of 28 to 30°C. The diet contained 206 g digestible crude protein and 14·2 MJ digestible energy per kg fresh weight. Three pigs failed to consume the total amount offered (offered 200 g/day for 2 days, consumed 49 g/day; offered 200 g/day for 2 days, consumed 80 g/day; offered 200 g/day for 4 days, consumed 135 g/day). Pigs remaining suckling their dams were also offered the diet as a freely available supplement.

After slaughter the animals were weighed and bled. Stomach, small intestine, large intestine and rectum were removed, and the digesta and excreta contained therein discarded. The empty gastro-intestinal tract was then placed together with the blood, lungs, liver, heart, spleen, gall bladder, pancreas, thymus, diaphragm, oesophagus, reproductive organs, flare fat, kidneys, head, feet and tail, to form the non-carcass (NC) fraction. The remaining carcass was divided longitudinally, and one half dissected into two fractions. The carcass fatty tissue (CFT) fraction comprised the skin, cutaneous trunci and subcutaneous fat. The remainder comprised the carcass intermuscular fat, muscle and bone (CMB) fraction. The three fractions were separately minced through a 1·5-mm plate, mixed, dried and analysed for ash, gross energy (GE) and nitrogen. Protein content was determined as N × 6·25 and lipid content as (GE −0·1475 N)/0·0393.

The empty body weight (EBW) (live weight (LW) less contents of intestinal tract) of pigs at the start of the experiment (day 0) was predicted from the determined composition of the unweaned pigs: NC = 0·289 (s.e. 0·004) LW; CFT = 0·186 (s.e. 0·004) LW; CMB = 0·503 (s.e. 0·014) LW. The chemical composition of live pigs at day 0 was similarly predicted from the determined composition of the unweaned pigs; coefficients are presented in Table 1. Regression constants were found to be not significantly different from zero and were suppressed. To assess the extent of lipid catabolism occurring, blood samples (10 ml) were taken from the aorta by venipuncture immediately prior to slaughter and free fatty acid (FFA) concentrations determined by the method of Wood, Gregory, Hall and Lister (1977).

RESULTS

The duration of the feed level treatment (2, 4, 6 or 8 days) had little effect on the daily empty body-weight gain (EBWG). Unweaned suckled pigs, as expected, maintained a constant level of live-weight gain, while for weaned pigs the reduced levels of gain pertaining over the whole trial period had been largely determined by day 2 (Figure 1).

There was, however, a significant effect of

TABLE 1

Coefficients giving the chemical composition of the live weight (LW), non-carcass (NC), carcass fatty tissue (CFT) and carcass muscle plus bone (CMB) of unweaned piglets

	LW	s.e.	NC	s.e.	CFT	s.e.	CMB	s.e.
Water	0·672	0·0046	0·734	0·0040	0·378	0·0128	0·736	0·0039
Lipid	0·155	0·0043	0·095	0·0031	0·511	0·0126	0·084	0·0024
Protein	0·149	0·0021	0·144	0·0028	0·104	0·0037	0·175	0·0028

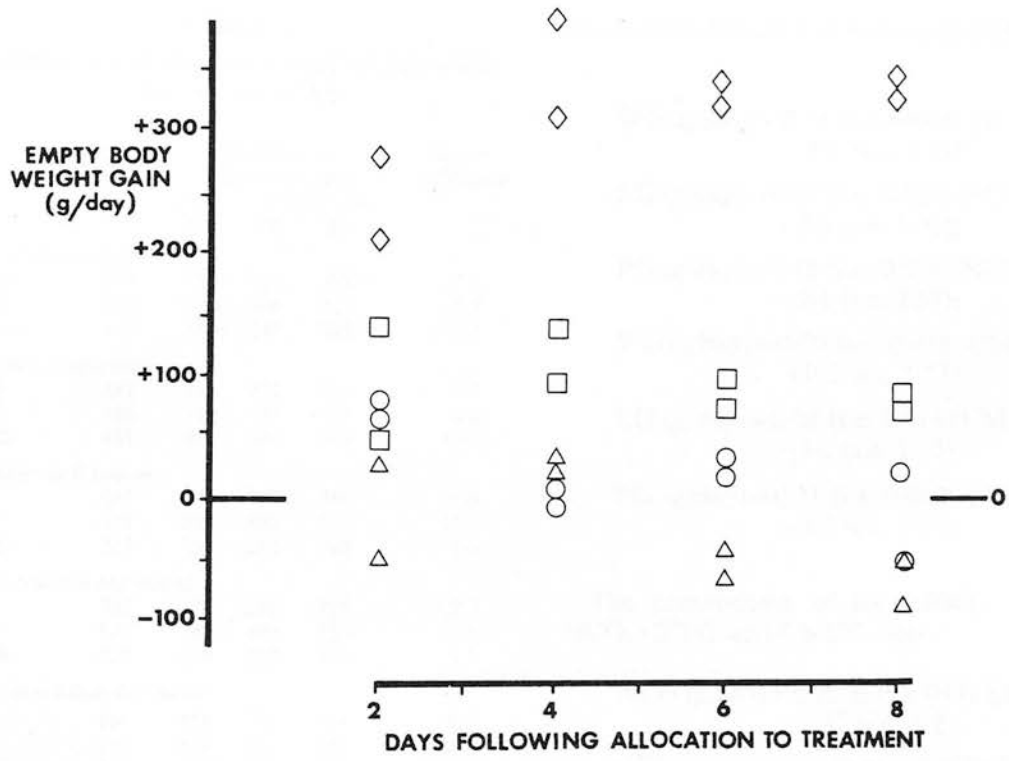

FIG. 1. Empty body-weight gains of pigs following allocation to treatment at 21 days of age (◇, suckled by dam; □, offered 200 g feed/day; ○, offered 100 g feed/day; △, offered 50 g feed/day).

weaned feed intake upon gain. Where F is daily feed intake:

$$\text{EBWG} = 0{\cdot}606 \text{ (s.e. } 0{\cdot}154) F - 25{\cdot}0 \text{ (s.e. } 18{\cdot}0).$$

The composition of the empty body was not influenced by the level of feed offered after weaning, but was greatly affected by weaning itself (Table 2). Weaned pigs contained more water and less lipid, more NC and less CFT. The lipid content of the CFT fraction was greatly reduced in weaned pigs and the dry-matter content of this fraction also decreased.

Figure 2 shows the reduction in daily empty body-weight gains which occurred following weaning and the reduced feed intake. Nevertheless, the pigs were able to maintain positive body-weight gains. Figure 3 illustrates that this pattern of body-weight change resulted from a combination of divergent responses. Lipid gains fell from nearly 50 g daily in the suckled pig to about −80 g daily at the 2nd day following weaning, to level off at −50 g to −25 g daily thereafter. Protein gains fell from nearly 50 g daily in the suckled pig to be slightly negative at the 2nd day following weaning, but the pigs returned to a positive protein balance thereafter. The relatively constant gains of empty body weight from the 2nd day following weaning (Figure 2) appear to have been maintained by the addition of water. Water gains remained positive and were sufficiently high at the 2nd day following weaning to more than counterbalance the lipid losses.

In Figure 4 the daily gains of the three dissected fractions in the weaned pigs are shown. NC tissues were consistently in positive balance, while CFT was being as equally consistently reduced. The CMB fraction was maintained narrowly in positive balance.

The carcass fatty tissue fraction gains (CFTG) of suckled pigs contained approximately equal amounts of lipid and water. After weaning, the losses of this fraction were characterized by simultaneous losses of lipid and gains of water (Figure 5). Over all pigs, the relationships

TABLE 2

Composition of the empty body of pigs when slaughtered (g/kg)

	Suckled by dam	Weaned and offered (g) daily			s.e. of difference
		200	100	50	
Chemical composition					
Water	674	710	714	705	5·7
Lipid	153	119	106	119	5·4
Protein	148	143	149	149	2·2
Fractional composition					
NC†	292	321	321	314	6·7
CFT	184	159	147	157	5·8
CMB	487	496	507	505	11·7
Dry matter in fractions					
NC	267	248	253	261	5·5
CFT	619	519	489	515	23·7
CMB	267	258	262	260	3·7
Lipid in fraction dry matter					
NC	352	322	305	328	12·7
CFT	821	760	694	723	21·1
CMB	235	236	222	233	8·7
Protein in fraction dry matter					
NC	534	558	575	565	11·0
CFT	172	259	294	244	37·2
CMB	649	628	640	637	6·1

†NC = non-carcass, CFT = carcass fatty tissue, CMB = carcass muscle and bone.

between CFTG and its chemical composition as water gain (WG), lipid gain (LG) and protein gain (PG) were:

$$\text{WG g/day} = 0{\cdot}16 \text{ (s.e. } 0{\cdot}053) \text{ CFTG} + 14{\cdot}8 \text{ (s.e. } 2{\cdot}56);$$

$$\text{LG (g/day)} = 0{\cdot}78 \text{ (s.e. } 0{\cdot}051) \text{ CFTG} - 17{\cdot}7 \text{ (s.e. } 2{\cdot}45);$$

$$\text{PG (g/day)} = 0{\cdot}06 \text{ (s.e. } 0{\cdot}011) \text{ CFTG} + 2{\cdot}9 \text{ (s.e. } 0{\cdot}54).$$

These show first that the fatty tissue gains comprised approximately 0·16 water, 0·78 lipid and 0·06 protein; and secondly, at zero CFTG a loss of 17·7 g lipid was balanced by gains of 14·8 g water and 2·9 g protein.

The equivalent equations for the chemical compositions of the non-carcass gains (NCG) and carcass muscle and bone gain (CMBG) were:

$$\text{WG (g/day)} = 0{\cdot}75 \text{ (s.e. } 0{\cdot}044) \text{ NCG} + 6{\cdot}0 \text{ (s.e. } 3{\cdot}11);$$

$$\text{LG (g/day)} = 0{\cdot}07 \text{ (s.e. } 0{\cdot}029) \text{ NCG} - 3{\cdot}5 \text{ (s.e. } 2{\cdot}02);$$

$$\text{PG (g/day)} = 0{\cdot}15 \text{ (s.e. } 0{\cdot}036) \text{ NCG} - 2{\cdot}1 \text{ (s.e. } 2{\cdot}57);$$

$$\text{WG (g/day)} = 0{\cdot}70 \text{ (s.e. } 0{\cdot}018) \text{ CMBG} + 9{\cdot}2 \text{ (s.e. } 1{\cdot}53);$$

$$\text{LG (g/day)} = 0{\cdot}08 \text{ (s.e. } 0{\cdot}014) \text{ CMBG} - 3{\cdot}1 \text{ (s.e. } 1{\cdot}15);$$

$$\text{PG (g/day)} = 0{\cdot}21 \text{ (s.e. } 0{\cdot}017) \text{ CMBG} - 8{\cdot}7 \text{ (s.e. } 1{\cdot}41).$$

The composition of the EBWG as dissected NCG, CFTG and CMBG were:

$$\text{NCG (g/day)} = 0{\cdot}20 \text{ (s.e. } 0{\cdot}033) \text{ EBWG} + 37 \text{ (s.e. } 5{\cdot}2);$$

$$\text{CFTG (g/day)} = 0{\cdot}31 \text{ (s.e. } 0{\cdot}037) \text{ EBWG} - 43 \text{ (s.e. } 5{\cdot}8);$$

$$\text{CMBG (g/day)} = 0{\cdot}49 \text{ (s.e. } 0{\cdot}038) \text{ EBWG} + 3 \text{ (s.e. } 5{\cdot}9).$$

These equations further suggested that at zero EBWG, NCG was approximately +37 g, CFTG was approximately −43 g, and CMBG was not significantly different from zero. CFTG became positive only at or above EBWG values of +139 g, while extrapolation suggests that NCG would only have become negative at or below EBWG values of −185 g.

The composition of EBWG as chemically analysed WG, LG and PG was:

$$\text{WG (g/day)} = 0{\cdot}56 \text{ (s.e. } 0{\cdot}040) \text{ EBWG} + 53 \text{ (s.e. } 6{\cdot}8);$$

$$\text{LG (g/day)} = 0{\cdot}29 \text{ (s.e. } 0{\cdot}039) \text{ EBWG} - 56 \text{ (s.e. } 6{\cdot}7);$$

$$\text{PG (g/day)} = 0{\cdot}15 \text{ (s.e. } 0{\cdot}015) \text{ EBWG} - 4 \text{ (s.e. } 2{\cdot}5).$$

These equations further suggested that at zero EBWG, WG was approximately +53 g, LG

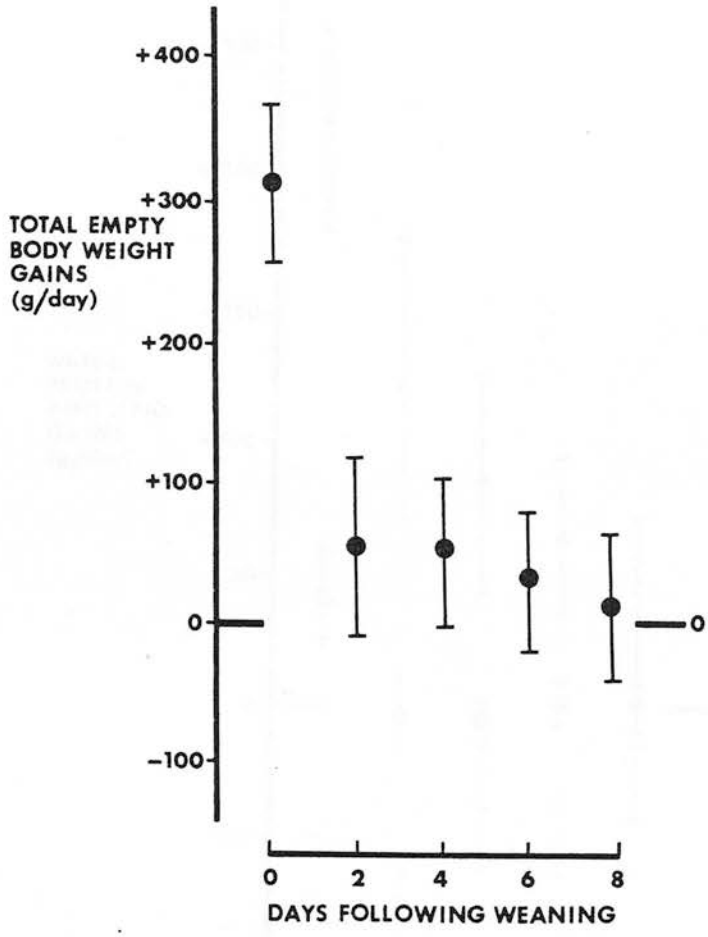

FIG. 2. Daily total empty body-weight gains of pigs following weaning (±s.d.).

approximately −56 g, and PG was not significantly different from zero. LG became positive only at or above EBWG values of +193 g, while WG only became negative at or below EBWG values of −95 g.

In the weaned pigs, lipid catabolism as assessed from plasma FFA concentrations was highest on day 2 (800 to 1500 μmol/l) and declined to day 8 (300 to 600 μmol/l). Pigs fed 50 g/day mobilized more fat than those fed 100 or 200 g. Where *D* is days on treatment:

offered 200 g
FFA (μmol/l) = 1056 (s.e. 51) − 85 (s.e. 9) *D*;

offered 100 g
FFA (μmol/l) = 1075 (s.e. 92) − 82 (s.e. 17) *D*;

offered 50 g
FFA (μmol/l) = 2227 (s.e. 318) − 221 (s.e. 58) *D*.

DISCUSSION

The pigs reponded to the reduction in feed intake within 2 days; there was a rapid deceleration of live-weight gain which stabilized at a low level thereafter. These slightly positive weight gains were associated with drastic reductions in body lipid. The weaned pigs catabolized lipid largely from the dissected subcutaneous fatty tissue, and the same tissue went some way to redress these losses by the retention of extra water. This response was only evident for CFT, but not for NC or CMB fractions. Changes in EBWG were associated

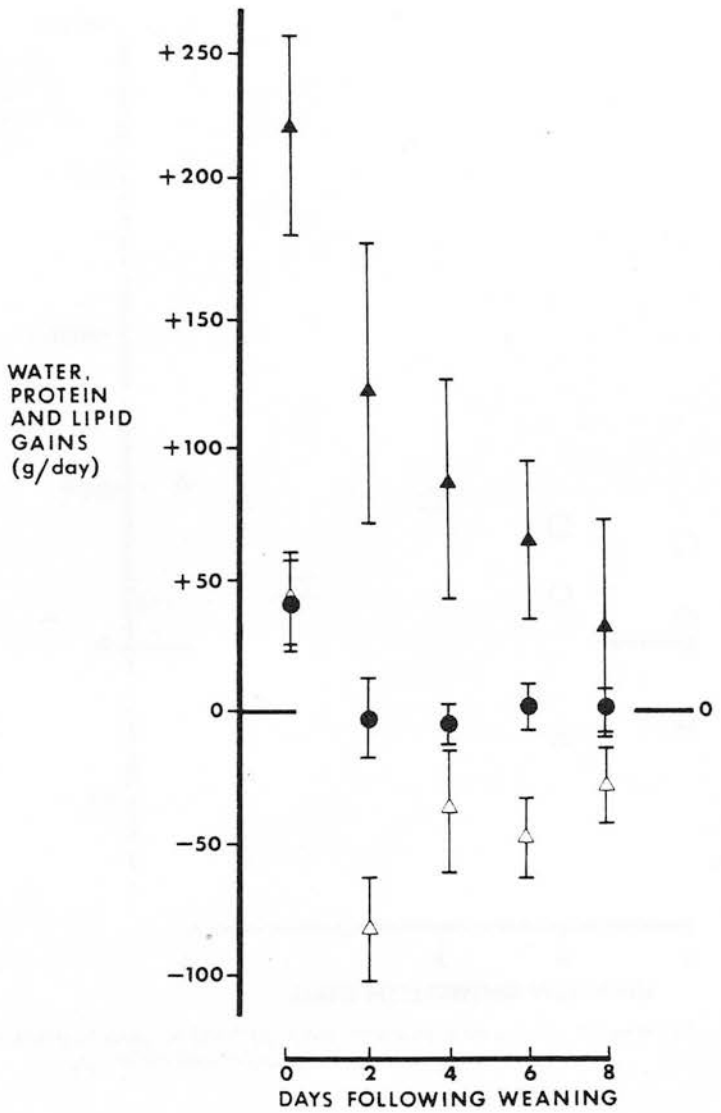

FIG. 3. Daily gains of water (▲), protein (●) and lipid (△) of pigs following weaning (±s.d.). Day 0 gains refer to the suckled control pigs.

with changes in CFT dry matter (DM) but not with changes in the DM of NC or CMB:

$$\text{NC DM} = 0{\cdot}004\ (\text{s.e. } 0{\cdot}002)\ \text{EBWG} + 25\ (\text{s.e. } 0{\cdot}4);$$

$$\text{CFT DM} = 0{\cdot}036\ (\text{s.e. } 0{\cdot}008)\ \text{EBWG} + 50\ (\text{s.e. } 1{\cdot}2);$$

$$\text{CMB DM} = 0{\cdot}002\ (\text{s.e. } 0{\cdot}001)\ \text{EBWG} + 26\ (\text{s.e. } 0{\cdot}2).$$

The rate of lipid losses as assessed both by tissue composition changes and by FFA concentrations decreased with time post weaning. This could have been an adaptive response or, more likely, because the extent of the depletion of the lipid reserves necessitated it. Levels of FFA at 2 days post weaning (800 to 1500 μmol/l) were similar to those observed in starved 50 kg pigs by Wood *et al.* (1977), showing that the young pigs at this stage could mobilize fatty acids as

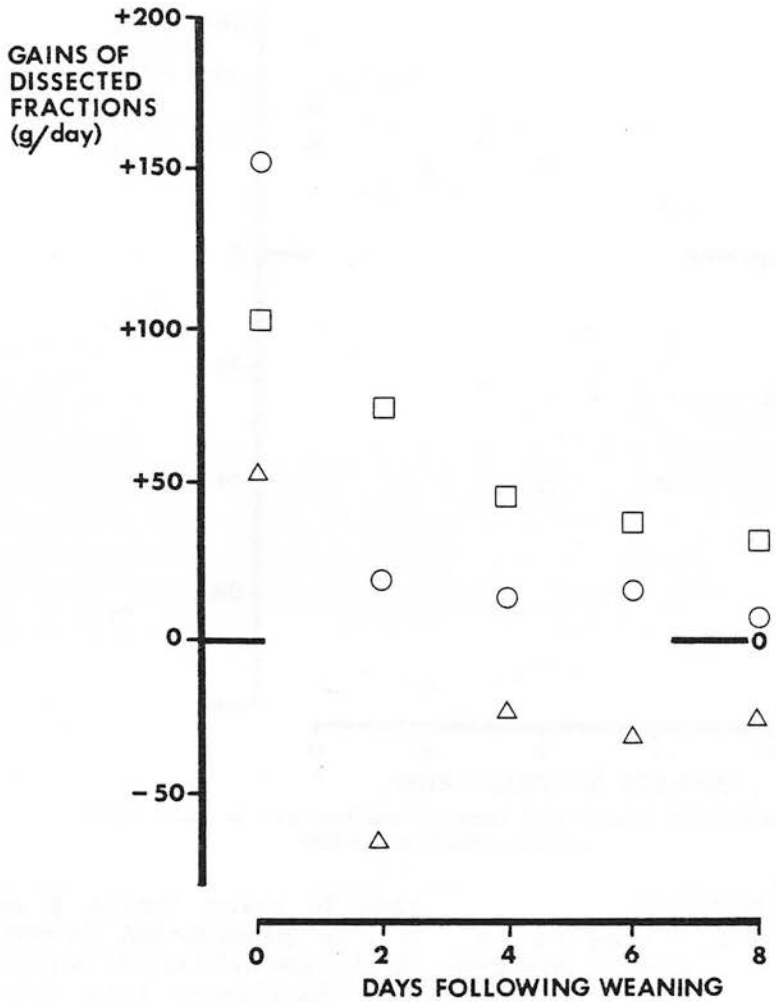

FIG. 4. Gains of dissected fractions of pigs following weaning. (□, Non-carcass; △, carcass fatty tissue; ○, carcass muscle and bone.)

effectively as older pigs. However, by 6 and 8 days post weaning FFA levels were much lower (300 to 600 μmol/l) suggesting a progressive failure to mobilize fat as the stores depleted. Both lipid losses and water gains seemed to be approaching zero at 10 to 12 days after weaning. After this time the pig could no longer survive on lipid reserves and, if still in negative energy balance, would need to resort to protein catabolism.

The animals achieved a high degree of protection for body protein, which remained in positive balance, and a constant proportion of EBW throughout. Evidence for this protection was the resistance to change shown in the muscle plus bone fraction (which remained in strict proportion to the empty body); while, perhaps most remarkably of all, the NC fraction actually continued to make positive gains while the fatty tissue was so rapidly diminishing. This can be interpreted as a clear case of protection, and even accretion, of the essential body parts at the expense of the non-essential.

The pigs would seem to begin to lose lipid at EBWG of approximately 193 g. This was as much as 66% of the gains of suckled pigs, and implies that unless they are growing almost as rapidly after weaning as before, young pigs are likely to be catabolizing lipid. This suggests (in common with Wood *et al.* (1977)) a rôle for fat

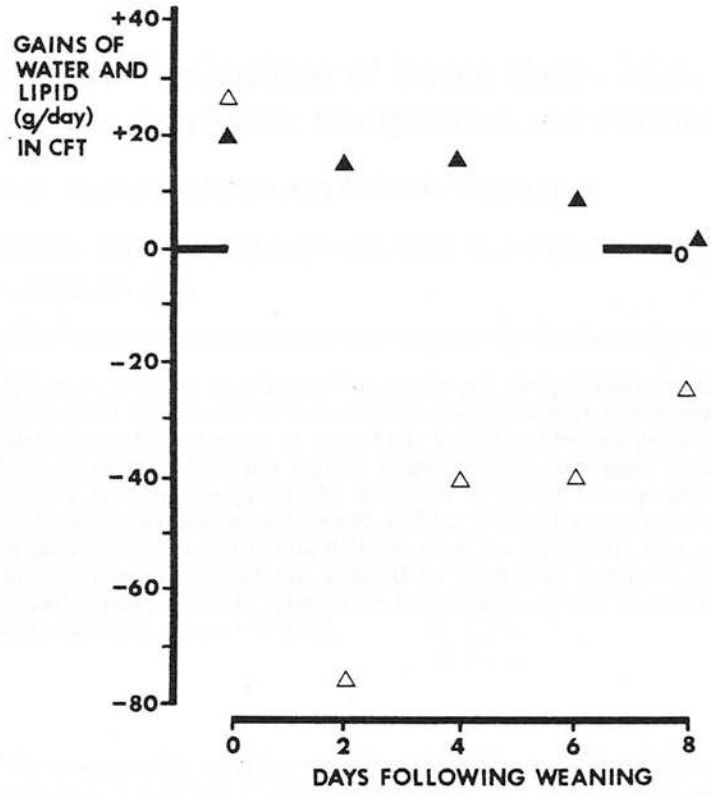

FIG. 5. Gains of water and lipid in carcass fatty tissue of pigs following weaning. (▲, Water; △, lipid.)

catabolism as a normal means of body composition control. Approximately 82% of CFT, 35% of NC and 24% of CMB was as lipid.

Zero EBWG were associated with counterbalancing gains of the NC and losses of CFT, and also with counter-balancing gains of water and losses of lipid. It is evident that, because of changes in water balance, the energy contribution of lipid metabolism cannot be judged from changes in live weight, nor even from changes in dissectible fatty tissue. Negative growth is clearly not the opposite to positive growth with regard to fatty tissue; but may be more nearly so for protein, which remained a constant proportion of the empty body weight regardless of the rate of gain or loss.

It is a reasonable objective for pig producers to sustain body condition and avoid catabolism of body tissue. To do this, pigs weaned at approximately 3 weeks of age require to maintain a growth rate in excess of about 200 g; this target is considerably above the achievement of current commercial practice in the post-weaning period.

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APPENDIX 2.3

Growth and Body Composition of Young Entire Male Pigs Fed Diets of Differing Ingredient Composition and Nutrient Quality

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Twenty-eight pairs of entire male Large White pigs of 5.59 kg liveweight were grown to 25 kg. They were offered two diets of different nutrient density and ingredient content: the diets (S and C) contained 16 and 15 MJ DE (digestible energy) and 235 and 214 g CP (crude protein) kg^{-1} dry matter, respectively. A liveweight of 25 kg was reached in 43.4 days by pigs given diet S and in 57.5 days by pigs given diet C ($P < 0.001$). Total feed intakes were 33.6 and 42.5 kg($P < 0.001$), respectively, but differences in daily feed intake (0.81 and 0.76 kg) were not significant. Chemical composition of the empty body was not affected by nutritional regime (12.4% lipid, 15.8% protein). The mean daily rates of protein deposition over the 5.59 to 25 kg growth phase were 64 g (S) and 55 g (C).

1. Introduction

The potential of the young pig for rapid growth is constrained by reduced nutrient intake following weaning. Weight stasis or weight loss at this time reflects a fall in lipid content of the body from 15% or more (at around 3 weeks of age) to 7% or less during the week after removal from the sow. Rate of recovery from this catabolic phase will be particularly influenced by nutrient intake and the energy:protein ratio of the diet.[1–3] Within 1 month of weaning, the lipid content of the body should have returned to approximately 10%.[3] Appetite, partially independent of the nutritional content of the diet, will affect total intake of nutrients and therefore largely governs the associated gain in liveweight and the tissue composition of that gain.

To assess the part played by nutrient supply during post-weaning growth, two diets of differing nutrient density, designated 'Special' (S) and 'Conventional' (C) (Super Kwik Wean and Kwik Wean Meal, RHM Agriculture Ltd), were fed to young pigs; entire males were chosen as being those animals most likely to respond favourably to higher quality diets.

2. Methods and materials

Twenty-eight littermate pairs of entire male Large White pigs were weaned at 21 days when their mean liveweight was 5.59 ± 0.139 kg. They were housed in individual wire-mesh cages with free access to water. One pig from each pair was offered diet S and the other offered diet C (Table 1). Both diets were in the form of a dry meal and all pigs were fed twice daily to appetite. Liveweight was measured weekly until pigs reached 25.0 ± 0.06 kg liveweight when 15 pairs were slaughtered; intestinal contents were removed and the whole empty body minced. Samples for chemical analysis were freeze-dried and milled, while the dry matter (DM) content was determined by oven-drying freshly-minced material. Gross energy was determined by adiabatic bomb, nitrogen by Kjeldahl digestion, and lipid by use of the equation:[3] $\text{Lipid} = (\text{GE} - 0.1475\text{N})/0.0393$ (assuming the energy content of protein and lipid to be 23.6 and 39.3 MJ kg^{-1}, respectively, and protein and lipid to be

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Table 1. Dietary composition and chemical analyses of experimental diets

Ingredient (kg t^{-1} freshweight)	Diet S	Diet C
Barley	109	500
Wheat	250	87
Flaked maize	265	100
Soya bean (extracted)	224	255
Fat premix (600 g kg^{-1})	60	22
Herring meal	50	—
Meat and bone meal	19	—
Avotan 20	2.0	2.0
Choline chloride	0.4	0.4
Salt	1.2	2.2
Limestone	2.0	5.6
Dicalcium phosphate	13.6	22.4
Minimix PG 360	3.5	3.5
DM (g kg^{-1} freshweight)	878.1	878.7
Composition kg^{-1} DM (calculated values given in parentheses)		
Gross energy (MJ)	18.85 ± 0.068	18.25 ± 0.076
Crude protein (g)	234.56 ± 1.744	213.50 ± 3.475
Lipid (g)	50.31	25.00
Ash (g)	61.62	60.77
Crude fibre (g)	60.55	62.22
DE (MJ)		
from ingredients	16.0	15.0
from diet specification	16.4	15.2
from TDN	16.6	15.0
DE (MJ):CP (g) ratio	1:14.7	1:14.2

Diets S and C, respectively (g kg^{-1} DM): Calcium: 1.012, 1.004. Phosphorus: 0.833, 0.842. Salt: 0.376, 0.386. Methionine + cystine: 0.750, 0.641. Lysine: 1.217, 1.057. Available phosphorus: 0.614, 0.581. Available lysine: 1.226, 1.053. Tryptophan: 0.435, 0.353. Threonine: 0.881, 0.759. Isoleucine: 1.110, 0.998.

the only energy-containing components in animal tissue). The chemical composition of pigs when weaned at 21 days was predicted by means of the regression equations shown in Table 2. Determined levels of crude protein were 235 and 214 g kg^{-1} DM for diets S and C, respectively, while calculated energy values were 16.0 and 15.0 MJ DE kg^{-1} DM.

Daily liveweight gains and feed intakes for individual pigs were calculated by regression of accumulated mass upon time; differences in growth and performance between pigs offered the two diets were assessed using a paired *t*-test for comparison of the difference between means.

Table 2. Chemical composition of pigs at 21 days of age[6]

Empty body weight (g) (EBW)	= 0.923 (± 0.0223) liveweight (g) + 140
Water (g)	= 0.647 (± 0.0223) EBW (g) + 177
Nitrogen (g)	= 0.0241 (± 0.00155) EBW (g) − 6.47
Lipid (g)	= 0.174 (± 0.0226) EBW (g) − 172
Ash (g)	= 0.0201 (± 0.00429) EBW (g) + 31
Gross energy (MJ)	= 0.0103 (± 0.00084) EBW (g) − 6.20

3. Results

Feed intakes and growth rates for pigs offered diets S and C are given in Table 3. Incidence of scouring was low on both diets. Weekly weights and liveweight gains are illustrated in Figure 1. Pigs offered diet S grew more rapidly, ate 8.9 kg less in total than pigs given diet C, and reached 25 kg liveweight an average of 14 days sooner. Daily liveweight gain and rate at which daily feed intake increased over time were both markedly greater for pigs offered diet S; mean daily feed intakes were not significantly different for the two diets, although the higher nutrient density of diet S resulted in a significantly enhanced intake of crude protein and digestible energy.

Table 3. Performance of entire male pigs grown from 5.59 to 25 kg liveweight

	Diet S	Diet C	Standard error of mean difference	Significance of difference
Days on test	43.6	57.6	2.23	***
Total feed intake (kg)	33.6	42.5	1.72	***
Daily liveweight gain (kg)	0.475	0.349	0.0190	***
Daily rate of increase of feed intake (kg)	0.032	0.022	0.0018	***
Daily feed intake (kg)	0.804	0.756	0.026	NS
Daily intake of CP (g)	160.4	139.1	3.74	***
Daily intake of energy (MJ DE)	10.94	9.78	0.259	***
Daily intake of energy kg^{-1} empty body weight (MJ)	0.475	0.448	0.0160	NS

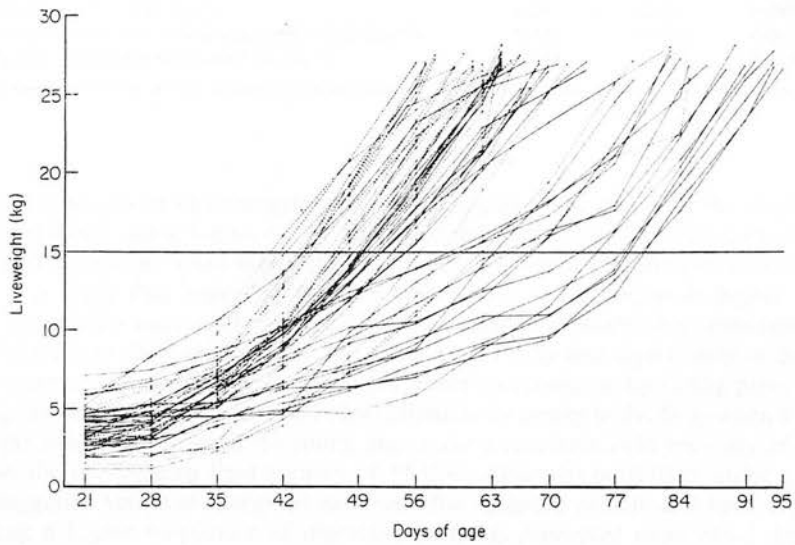

Figure 1. Weekly weights (kg) and liveweight gains by young entire male pigs fed diet S,– – – –, Special ($n=28$); C, ———, Conventional ($n=28$).

Total feed intake (kg) = 70.4 (±2.83) − 80.5 (±6.90) daily liveweight gain (kg), showing that an increase in daily liveweight gain was associated with a decrease in total feed consumed, reflecting the relative digestibilities of the two diets and increased maintenance costs accruing from slower growth on diet C. The relationship between total feed intake (Y kg) and days on test (X) varied with the nutrient density of the diet such that the slope for diet S had a lower gradient, and a greater constant when compared to diet C:

Diet S $Y=0.407\ (\pm 0.0615)X+16.0\ (\pm 2.70)$
Diet C $Y=0.620\ (\pm 0.0860)X+6.83\ (\pm 5.031)$

Pigs fed diet C showed much greater variation in performance, notably with respect to time taken to reach 25 kg liveweight (s.d.: diet S 6.5, diet C 11.2). Daily feed intake (X kg) was a good predictor of daily liveweight gain (Y kg) for pigs fed diet S [$Y=0.626\ (\pm 0.0838)X-0.033\ (\pm 0.0658)$], but not for pigs fed diet C [$Y=0.092\ (\pm 0.1677)X+0.278\ (\pm 0.1258)$], showing the diet of higher nutrient density to be a more important causative factor of growth in early-weaned pigs.

There was no effect of diet upon chemical composition of the empty body of pigs at 25 kg liveweight (Table 4). Pigs given diet S deposited considerably more protein daily than pigs given diet C (63.6 *vs* 54.9 g), but efficiencies of protein and energy utilisation did not differ between the two diets (Table 4).

Table 4. Chemical composition of the empty body of 25 kg entire male pigs and efficiency of utilisation of nutrients

	Diet S	Diet C	Standard error of mean difference	Significance of difference
Empty body weight (kg)	22.54	21.61	0.171	***
Daily gain in empty body (kg)	0.393	0.327	0.0106	***
Energy in empty body (MJ GE)	190.5	189.3	3.93	NS
Lipid in empty body (kg)	2.73	2.72	0.101	NS
Protein in empty body (kg)	3.52	3.49	0.056	NS
Protein retention (g day^{-1})	63.3	54.9	1.95	***
Energy retention (MJ GE day^{-1})	3.26	2.80	0.098	***
Energy retained (MJ day^{-1})/DE consumed (MJ day^{-1})	0.302	0.292	0.0077	NS
Protein (g day^{-1})/Protein consumed (g day^{-1})	0.398	0.386	0.0148	NS

4. Discussion

Total feed intake to 25 kg liveweight was lower for pigs given diet S; of the extra 8.9 kg eaten by pigs offered diet C, some 5–6 kg can be attributed to increased maintenance costs over the extended growth period. As diet S had little advantage in terms of energy:protein ratio (1:14.7 *vs* 1:14.2 for diet C) it is likely that improved performance on diet S was due to its higher nutrient quality, greater digestibility and, most importantly, to an enhanced palatability stimulating a more rapid rate of increase in daily feed intake. The lower palatability and digestibility of diet C would also tend to increase variation in feed intake, and hence performance, by young pigs offered this diet.[5] At 25 kg liveweight, all pigs contained 12.4% lipid in the empty body. Only when a diet of narrower energy:protein ratio is offered do young pigs make a relatively swift recovery of lipid reserves to return to the pre-weaning lipid content of 15%.[3,4] Although both diets under consideration fell within suggested values of energy:protein ratio for optimum protein and lipid deposition, the diet containing a higher proportion of digestible nutrients promoted more rapid deposition of both protein and lipid. Differences in the pattern of growth between pigs fed diet S and those fed diet C were most apparent in the first part of the trial period, there being 12 days' difference in time taken to grow from the start of the trial to 15 kg liveweight (diet S 28 days, diet C 40 days, s.e. = 2.1, $P<0.001$). However, there was only 3 days' difference in the time taken to grow from 15 to 25 kg liveweight (diet S 15 days, diet C 18 days, s.e. 0.9, $P<0.01$). This difference in response would suggest that it was particularly in the early growth phase that the greater nutrient density and palatability of diet S was of most benefit to the digestive physiology of young pigs. Inclusion in diet S of extra wheat, cooked starch (flaked maize) and animal protein brought about a reduction in fibre content of 0.28% and increased digestible energy by 6.7%; this relatively minor improvement in nutrient density was responsible for a marked difference in growth rate during the 14 days,

post-weaning. The superiority of this diet over diet C in terms of growth rate of young pigs may owe more to enhanced palatability and digestibility of the protein and energy fractions than to energy:protein ratio and nutrient concentration *per se*.

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Efficiency of use of nitrogen from dried microbial cells after a period of N deprivation in growing pigs

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1. Semi-synthetic diets, with dried microbial cells (Pruteen) as the nitrogen source, were used to measure N retention in 50 kg pigs which had been given only sufficient N (5·3 g/d) to maintain N equilibrium for the previous 12 d. Control pigs were given 33·2 g N/d.

2. Metabolic faecal N losses were 1·62 g/d (1·2 g/kg dry matter eaten) and endogenous urinary losses were 3·90 g/d.

3. Realimentation of N-deprived pigs was achieved with diets providing 20·0, 33·2 and 67·4 g N/d and daily rates for N retention were 11·2, 17·8 and 25·9 g respectively; the corresponding value for control pigs was 15·0 g. 'Catch-up' protein growth was demonstrated in pigs given both 33·2 and 67·4 g N/d. In the former instance, this was associated with an increase in the efficiency of utilization of dietary N.

4. The biological value of the protein in Pruteen was 0·85, and it appeared that under conditions of increased demand for N the pig could utilize some of the nucleic acid-N fraction of this protein source.

Reduced growth consequent upon food deprivation may be subsequently made good by 'catch-up' growth (Allden, 1970; Fowler, 1976). There is dispute, however, as to the tissues involved in 'catch-up' growth and whether or not there is a change in metabolic efficiency. Fowler (1976) distinguishes between 'target' and 'variable' fat, the latter being a function of the level of energy supply in excess of the physiological needs for growth of lean and essential tissues. Growth fluctuations in 'variable' fat, dictated by changes in food supply, are of less significance than those in lean tissue. If protein retention in lean growth reacts to nutrient supply in the same way as 'variable' fat, 'catch-up' growth in all tissues would follow automatically upon realimentation. The contrary is more likely to be the situation however, as protein growth is also subject to physiological control.

Kielanowski (1969) is of the opinion that enhanced protein retention can be an integral part of 'catch-up' growth, and this has recently been demonstrated by Fowler (1976). Other recent reports of 'catch-up' growth (e.g. Laksesvela, 1976; Neilsen, 1976) are more difficult to interpret as the tissues concerned are not identified, and responses could have been exclusively in the form of 'variable' fat.

'Catch-up' protein growth, where treated animals show enhanced protein retention greater than that of non-deprived control animals, implies either an increase in protein supply above the control level or an increase in the efficiency of use of the same protein supply. The latter phenomenon would require an improvement in effective biological value (BV) of dietary protein. Millward, Garlick, James, Sender & Waterlow (1976) have expressed the belief that the decrease in nitrogen excretion after N deprivation is partly as a result of a reduction in the proportion of the flux excreted. It appears from the results of Millward, Garlick & Nnanyelugo (1974) that although refeeding effects an increase in flux, there is a delay of approximately 14 d in the instance of the rat, during which it is conceivable that protein retention may occur concomitant with a less than commensurate excretion rate, thus enabling an increase in effective BV.

Information about the efficiency of protein use as evidenced by BV is a prime considera-

Table 1. *Chemical composition (g/kg dry matter (DM)) of dietary ingredients*

Ingredient	DM (g/kg)	Gross energy	Nitrogen	Fat	Fibre	Ash
Dried microbial cells*	893	22·57	122·55	86·00	16·40	88·19
Maize starch	864	17·08	0·50	0·81	5·60	1·52
Sucrose	999	16·40	0·17	2·00	4·00	0·36
Glucose	911	15·52	0·17	2·40	2·80	0·64
Cellulose†	936	17·24	0·21	0·0	35·21	4·24
Maize oil	0	39·70	0·0	99·92	0·0	0·0
Mineral and vitamin mixture‡	910	—	1·82	3·60	4·80	895·55

* Pruteen; ICI Ltd (Agricultural Division), Billingham, Cleveland.

† Solka-floc; Johnson, Jorgenson and Wettre Ltd, London EC4M 7HA.

‡ 1065C; Vitriton Ltd, Stamford, Lincs PE9 2RA. To supply (/kg diet); calcium 11·8 g, phosphorus 8·0 g, sodium chloride 5·0 g, potassium 5·0 g, magnesium 400 mg, iron 60 mg, zinc 60 mg, manganese 20 mg, copper 10 mg, cobalt 0·5 mg, iodine 0·8 mg, thiamin 4·0 mg, riboflavin 5·0 mg, nicotinamide 30·0 mg, pantothenic acid 10·0 mg, pyridoxine 2·5 mg, pteroylmonoglutamic acid 2·0 mg, choline 1000 mg, cyanocobalamin 20·0 μg, retinol 901 μg, biotin 200 μg, cholecalciferol 25·0 μg, D-α-tocopherol 10·0 mg, menaphthone 120 μg, butylated hydroxytoluene 0·125 g.

tion in the evaluation of a new food protein. There are few estimates of BV for the dried microbial cell (DMC) protein source used here, and those are not wholly in agreement. Schulz & Oslage (1976) determined a BV of 0·79 with rats, whereas D'Mello, Peers & Whittemore (1976) found 0·68 with young growing pigs. The potential utilization by pigs of the non-amino nucleic acid-N fraction of DMC (comprising 0·19 of the total DMC N), remains unresolved (D'Mello *et al.* 1976), but nevertheless is of relevance to BV determinations.

N retention and efficiency of use of protein from DMC are studied here by conventional balance techniques after 10 d deprivation and 20 d realimentation at three levels of N supply. The evidence presented will show that enhanced N retention can occur after N deprivation and that this can be consequent upon an increase in efficiency of N use.

EXPERIMENTAL

Diets

Four semi-synthetic diets were compounded from the ingredients whose composition is shown in Table 1. The protein source was DMC (Pruteen; ICI Ltd (Agricultural Division), Billingham, Cleveland), which is the flash-dried product of the culture of *Methylophilus methylotrophus* on methanol. The amino acid composition of the N in DMC is given in Table 2. Ingredients were compounded in the proportions indicated in Table 3, to form four diets of differing N content. Determined N contents were 3·92, 14·78, 24·28 and 49·98 g/kg dry matter (DM) for diet nos. 1–4 respectively. All diets were fed at the rate of 750 g twice daily together with 1·5 l water at each feed. There were no refusals. Daily intakes of DM, gross energy (GE) and N are presented in Table 4. Diet no. 1 was formulated to maintain the animals in N equilibrium, while diet no. 3 was calculated to approach the animal's requirement.

Procedures

Twenty-three Large White × Landrace barrows of 49·2 ± 1·32 (mean ± SE) kg live weight were used for conventional N balance determinations using metabolic crates which allowed quantitative feeding and the separate collection of faeces and urine. Bulk 10 d or 5 d collections of excreta were preserved at pH 3–3·5 by addition of dilute sulphuric acid, and analysed for N by the Kjeldahl technique and for GE by adiabatic bomb calorimetry.

All pigs were given diet no. 3 for 3 d before the start of the experiment, and then six

Table 2. *Amino acid composition (g/16 g nitrogen) and N contents (g/kg* DM*) of dried microbial cells**

	Source			
Amino acid	D'Mello, Peers & Whittemore (1976)	ICI Ltd (1976)	ICI Ltd (unpublished results)	Schulz & Oslage (1976)
Aspartic acid	9·2	8·6	8·3	—
Threonine	4·9	4·6	4·2	4·2
Serine	3·2	3·4	3·4	—
Glutamic acid	12·7	9·8	9·7	—
Glycine	7·0	5·1	5·3	5·0
Alanine	7·4	6·9	7·2	—
Valine	6·0	5·3	5·1	5·2
Cystine	0·8	0·6	—	3·6
Methionine	2·3	2·5	2·1	
Isoleucine	4·1	4·4	4·2	4·4
Leucine	6·9	6·8	6·9	7·0
Tyrosine	4·1	3·1	2·8	—
Phenylalanine	5·2	3·5	3·2	—
Lysine	5·6	6·3	5·8	5·9
Histidine	1·9	2·0	1·7	1·7
Arginine	4·6	4·5	4·4	4·5
Tryptophan	0·9	1·0	—	—
N component				
Total N	129·9	128·0	127·0	131·0
Nucleic acid-N	24·2	24·0	24·3	—
N recovered as amino acids	96·3	104·0	—	—
Ammonia	—	0·08	0·15	—

DM, dry matter.
* Pruteen; ICI Ltd (Agricultural Division), Billingham, Cleveland.

Table 3. *Ingredients (g/kg fresh weight) and chemical composition of experimental diets fed to pigs*

	Diet no.			
Ingredients	1	2	3	4
Dried microbial cells*	24·75	95·50	185·00	370·00
Maize starch	725·25	657·50	565·00	380·00
Sucrose	50·00	50·00	50·00	50·00
Glucose	50·00	50·00	50·00	50·00
Cellulose	30·00	30·00	30·00	30·00
Maize oil	50·00	50·00	50·00	50·00
Vitamins and minerals†	70·00	70·00	70·00	70·00
Chemical composition				
DM (g/kg)	904·3	902·2	910·7	917·5
Gross energy (MJ/kg DM)	16·22	17·14	17·49	18·77
Nitrogen (g/kg DM)	3·92	14·78	24·28	49·98

DM, dry matter.
* Pruteen; ICI Ltd (Agriculture Division), Billingham, Cleveland.
† For details, see Table 1.

Table 4. *Daily intakes of dry matter* (DM), *gross energy* (*GE*) *and nitrogen by pigs given experimental diets of differing nitrogen content**

	Diet no.			
	1	2	3	4
Fresh wt (g/d)	1500·0	1500·0	1500·0	1500·0
DM (g/d)	1356·0	1353·3	1366·3	1376·3
GE (MJ/d)	21·98	23·19	23·90	25·84
N (g/d)	5·31	20·00	33·17	67·41

* For details, see Tables 1–3.

Table 5. *Design of experiment to determine the effect of feeding diets of differing nitrogen content** (*diet nos.* 1–4) *to pigs after a period of N deprivation*

Day of experiment	Balance period no.	Dietary treatment				
		3-3	1-1	1-2	1-3	1-4
1–2	—	3	1	1	1	1
3–12	1	3	1	1	1	1
13–14	—	3	1	2	3	4
15–19	2	3	1	2	3	4
20–24	3	3	1	2	3	4
25–29	4	—	—	—	3†	4†
30–34	5	—	—	—	3†	4†
No. of pigs		6	5	4	4	4

* For details of diets, see Tables 1–4.
† Two pigs for each dietary treatment.

pigs were allocated to diet no. 3 and the remainder to diet no. 1 for a preliminary feeding period of 2 d. From the third to the twelfth day, a 10 d balance period (balance period no. 1) was completed, after which six pigs remained on diet no. 3 (treatment 3-3), five pigs remained on diet no. 1 (treatment 1-1), while four pigs were each allocated to diet nos. 2 (treatment 1-2), 3 (treatment 1-3) and 4 (treatment 1-4) for a further preliminary feeding period of 2 d. There were two 5 d balance periods from the fifteenth to the twenty-fourth day of the trial; balance period no. 2 days 15–19, balance period no. 3 days 20–24. Two pigs each remained on diet nos. 3 and 4 for a further two 5 d balance periods; balance period no. 4 days 25–29, balance period no. 5 days 30–34 (see Table 5).

RESULTS

Daily N losses from pigs given diet no. 1 (dietary treatment 1-1: balance period no. 1, seventeen pigs; balance periods nos. 2 and 3, five pigs) were (mean ± SE) 1·62 ± 0·089 g in faeces and 3·90 ± 0·147 g in urine. These were assumed to be measurements of metabolic faecal N (MFN) and endogenous urinary N (EUN) losses. Equivalent losses for pigs given diet no. 3 (dietary treatment 3-3: balance period no. 1, six pigs; balance periods nos. 2 and 3, six pigs) were (mean ± SE) 2·65 ± 0·126 g and 15·48 ± 0·972 g.

Table 6 gives the N retention and digestibilities in balance period no. 1 (days 3–12) for pigs given diet nos. 1 (5·31 g N/d) and 3 (33·2 g N/d). The N retention found for pigs given diet no. 1 (−0·32 ± 0·439 g/d) showed the animals to be close to N balance. Apparent N digestibility ((N intake − faecal N) ÷ N intake) of diet no. 1 was reduced due to the high loading of MFN in comparison to N intake; determination of true digestibility ((N intake -

Table 6. *Nitrogen retention and digestibility of gross energy (GE) and N in balance period no.* 1 *(days* 3–12 *of the experiment)*† *for pigs given diet nos.* 1 *and* 3. *Diet nos.* 1 *and* 3 *contained* 3·9 *and* 24·3 *g N/kg dry matter respectively*‡

(Mean values with their standard errors for seventeen animals (diet no. 1) and six animals (diet no. 3))

	Diet				Statistical significance of difference between treatments
	1		3		
	Mean	SE	Mean	SE	
N retention (g/d)	−0·32	0·317	15·06	0·534	***
Digestibility					
GE (apparent)	0·95	0·003	0·95	0·005	NS
N (apparent)	0·65	0·013	0·91	0·022	***
(true)	0·96	0·013	0·96	0·022	NS

NS, not significant.
*** $P < 0·001$.
† For details of experimental procedures, see Table 5.
‡ For details of diets, see Tables 1–4.

Table 7. *Nitrogen balance and digestibility of gross energy (GE) and N in balance periods nos.* 2 *and* 3† *(days* 15–24 *of the experiment) for pigs given dietary treatments* 3-3, 1-2, 1-3 *and* 1-4. *Diet nos.* 1, 2, 3 *and* 4 *contained* 3·9, 14·8, 24·3 *and* 50·0 *g N/kg dry matter respectively*‡

(Mean values for six animals (treatment 3-3) and four animals (other treatments))

	Dietary treatments				SE of treatment means		Statistical significance of difference between treatments
	3-3	1-2	1-3	2-4	Treatment 3-3	Other treatments	
N balance							
N retention (g/d)	15·04	11·19	17·77	25·86	0·996	1·220	***
N retained ÷ digested N	0·49	0·62	0·58	0·41	0·022	0·027	***
Biological value §	0·64	0·85	0·72	0·49	0·020	0·025	***
Digestibility							
GE (apparent)	0·96	0·96	0·95	0·93	0·004	0·005	***
N (apparent)	0·93	0·90	0·93	0·95	0·006	0·007	**
(true)	0·97	0·98	0·98	0·96	0·006	0·008	NS

NS, not significant.
** $P < 0·01$, *** $P < 0·001$.
† For details of experimental procedures, see Table 5.
‡ For details of diets, see Tables 1–4.

§ BV $= \dfrac{\text{N intake} - (\text{faecal N} - \text{MFN}) - (\text{urinary N} - \text{EUN})}{\text{N intake} - (\text{faecal N} - \text{MFN})}$, where MFN is metabolic faecal N, EUN is the endogenous urinary N.

faecal N + MFN) ÷ N intake) showed the N from both diets to be equally effectively absorbed.

N utilization in balance periods nos. 2 and 3 (days 15–24) is shown in Table 7. There were no differences between results for the two balance periods, and the mean values of results for individual pigs are given. True digestibility of N remained unaffected by dietary treatment ($P > 0·05$). Pigs given dietary treatment 3-3 (33·2 g N/d) continued to retain 15·0 g N/d, with an apparent digestibility coefficient for N of 0·93 and a true digestibility coefficient for N of 0·97. The efficiency of N retention (N retained ÷ apparently digested N) was 0·49 and the BV was 0·64.

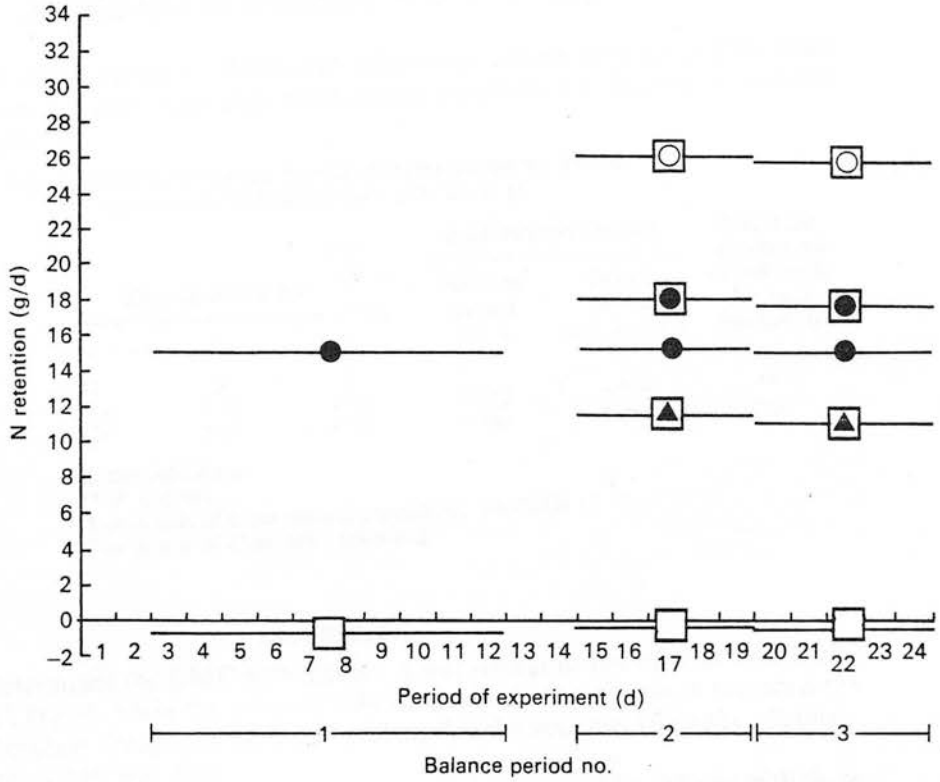

Fig. 1. Nitrogen retention (g/d) in balance periods nos. 1, 2 and 3 for pigs given dietary treatments 1-1 (□) (deprivation); 3-3 (●) (control); 1-2 (▲); 1-3 (◉), 1-4 (◎) (deprivation in balance period no. 1, followed by realimentation in balance periods nos. 2 and 3). Diet nos. 1, 2, 3 and 4 contained 3·9, 14·8, 24·3 and 50·0 g N/kg DM respectively. For details of diets and experimental procedures, see Tables 1–5 and p. 194.

Values for N retention by pigs throughout 34 d of N balance determinations are shown in Fig. 1.

The influence of N deprivation in pigs given diet no. 1 in balance period no. 1, on N balance in pigs given diet nos. 2, 3 and 4 in balance periods nos. 2 and 3 was to enhance the rate of N retention. Dietary treatment 1-3 effected a net increase of 2·73 g N/d in excess of that of dietary treatment 3-3 ($P < 0·05$). By comparison with diet treatment 3-3, the N from dietary treatment 1-3 was utilized with significantly greater efficiency (0·58 *v.* 0·49, $P < 0·05$) and had a higher BV (0·72 *v.* 0·64, $P < 0·05$) (see Table 7). Dietary treatment 1-2 had the highest value for efficiency of N utilization (0·62) and the BV of the N was 0·85. The level of N intake by pigs given diet no. 2 (20·0 g N/d) was below the requirement of the pig as evidenced by responses to diet no. 3; efficiencies found for diet no. 2 would therefore appear to have been representative of maximum values for the DMC N source. Pigs given dietary treatment 1-4 (67·4 g N/d) showed the highest rate of N retention (25·9 g N/d) but efficiency of utilization was markedly reduced.

N balances for two pigs each given dietary treatments 1-3 and 1-4 were continued for a further 10 d (balance periods nos. 4 and 5) to measure responses up to 22 d after deprivation. Enhanced retentions were still evident at average values of 18·7 and 29·2 g N/d for dietary treatments 1-3 and 1-4 respectively.

Table 8. *Metabolic faecal nitrogen (MFN) and endogenous urinary nitrogen (EUN) losses in balance periods nos.* 1, 2 *and* 3† *for pigs given dietary treatment* 1-1. *Diet no.* 1 *contained* 3·9 *g N/kg dry matter*‡

(Mean values for seventeen animals (balance period no. 1) and five animals (balance periods nos. 2 and 3))

	Balance period no.			SE of treatment means		Statistical significance of difference between treatments
	1	2	3	Balance period no. 1	Balance periods nos. 2 and 3	
No. of pigs	17	5	5			
MFN	1·84	1·27	1·23	0·073	0·135	***
EUN	3·86	3·76	4·17	0·127	0·235	NS

NS, not significant.
*** $P < 0.001$.
† For details of experimental procedures, see Table 5.
‡ For details of diets, see Tables 1–4.

DISCUSSION

The BV of 0·64 determined for DMC with diet no. 3 was similar to the value of 0·68 found by D'Mello *et al.* (1976), while the value of 0·85 determined with diet no. 2 exceeded the value of 0·79 of Schulz & Oslage (1976). It was evident that the potential efficiency of utilization of N from the DMC was high.

Values for MFN and EUN of 1·62 and 3·90 g/d respectively should be collated with those of 1·11 and 2·91 g/d measured by D'Mello *et al.* (1976) and 3·2 g/d for EUN measured by Lubaszewska, Pastuszewska & Kielanowski (1973) in pigs of similar weight. Lubaszewska *et al.* (1973) noted an increase in EUN with duration of protein deprivation. When expressed on a per unit food intake basis, Whiting & Bezeau (1957) found MFN to be 1·0 g/kg DM and Armstrong & Mitchell (1955) reported a value of 1·1 g/kg DM; the equivalent value for the present experiment was 1·2 g/kg DM. MFN was less and EUN tended to be greater in balance period no. 3 as compared to balance period no. 1 (Table 8) although the difference was not significant for EUN. The influence of the duration of deprivation on MFN and EUN was considered insufficient to merit use of individual values for each balance period, rather than the mean value, for determination of true digestibility and BV. The significantly higher MFN value measured in balance period no. 1 was quantitatively small, and may be attributable to 'carry-over' effects from the preliminary feeding period.

Comparison of dietary treatment 3-3 with dietary treatment 1-4 showed enhanced protein growth (N retention (g/d) 15·0 *v.* 25·9) during realimentation with ample protein; lost protein growth would be recouped in 12 d. Comparison of dietary treatment 3-3 with dietary treatment 1-3 demonstrates 'catch-up' protein growth in the strictest sense (N retention (g/d) 15·0 *v.* 17·8) together with simultaneously enhanced efficiency of protein utilization; there being no increase in dietary protein supply (efficiency of retention, 0·49 *v.* 0·58; BV, 0·64 *v.* 0·72). In this instance, lost protein growth would be recouped in 7 weeks.

The increase in efficiency was mediated through a reduction in the rate of urinary N loss. This could have resulted from a deceleration of protein catabolism or an increase in anabolic efficiency associated with protein turnover. Alternatively, there could have been an increase in the proportion of absorbed protein utilized. A decrease in catabolism, elicited by protein deprivation and sustained into the realimentation phase, is consistent with responses found in rats (Millward *et al.* 1976). The phenomenon is, however, probably

too slow-acting to be entirely responsible for the present result. Further, a reduction in the rate of protein turnover might have been expected to have caused a progressive reduction in EUN, but this did not occur: values for EUN suggested a response which was complete within the 2 d preliminary feeding period and more akin to a 'shutdown' of the urea cycle, an increase in the efficiency of anabolism and a reduction in the proportion of catabolized protein which was excreted. Das & Waterlow (1974) showed how the protein-deprived rat could in this way reduce N excretion by 75% in 30 h. Conversely, while the 'carry-over' effects of a decrease in catabolic rate are evident (Millward *et al.* 1976), it is not conceivable that 'shutdown' of urea synthesis would be maintained throughout the 20 or more d of realimentation feeding, for which period this experiment demonstrated enhanced BV.

The most plausible explanation for the enhanced BV with dietary treatment 1-3 would be an increase in the proportion of the constituents of the dietary protein utilizable by the pig. D'Mello *et al.* (1976) proposed some part of the nucleic acid fraction of DMC to be available to the animal. The availability of this fraction may be related to the extent of the animal's need, the latter being greater after protein deprivation. Of the N contained in DMC approximately 19% is nucleic acid-N. Subtraction of the appropriate proportion of nucleic acid-N from the various elements of the BV determination allows a calculation of BV on the assumption that none of the nucleic acid-N is utilized. Such calculations for dietary treatments 1-2 and 1-3 give BV values of 1·04 and 0·87 respectively, which indicates that either DMC protein is of quite exceptional quality or that some of the nucleic acid-N is usable by the pig.

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APPENDIX 3.2: Nitrogen balance and digestibility coefficients in balance periods 2A (3 days) and 2B (7 days) for pigs given a change of dietary nitrogen intake from the end of balance period 1 (diet controls are provided for comparison)

	Balance period	Diet No. 1			Diet No. 2			Diet No. 3				Diet No. 4		SE of difference between: (i) diets for pigs changed to higher nitrogen	(ii) balance periods 2A and 2B	(iii) treatments within diets for balance period 2B
		1-1-1	2-1-2	3-1-3	2-2-2	1-2-2	1-2-1	3-3-3	1-3-3	1-3-1	2-3-3	4-4-4	1-4-4			
No. of pigs	2A	3[1]	4	4	3[2]	4	4	4	4	4	3[3]	4	4			
	2B	3[1]	4	4	4	4	4	4	4	4	4	4	4			
Nitrogen retention (g day^{-1})	2A	0.98	0.74	-0.11	19.48	19.54	19.42	23.93	29.12	27.34	33.60	33.34	39.08	1.400[4]	1.980[7]	
	2B	0.74	0.89	1.84	16.62	17.76	17.96	23.20	30.05	28.15	29.52	33.43	37.72	1.212[5]***	1.715[8] NS	3.911* Diet 3 only
														0.990[6]	1.400[9]	
Nitrogen retained ÷ nitrogen digested	2A	0.19	0.16	-0.03	0.66	0.67	0.66	0.41	0.49	0.48	0.59	0.38	0.44	0.025	0.036	
	2B	0.16	0.14	0.34	0.59	0.62	0.63	0.42	0.58	0.50	0.52	0.38	0.42	0.022***	0.031 NS	0.102 NS
														0.018	0.025	
Biological value	2A	1.00	1.00	0.87	0.81	0.82	0.81	0.50	0.57	0.56	0.67	0.43	0.50	0.025	0.035	
	2B	1.02	1.03	1.06	0.75	0.78	0.78	0.51	0.66	0.58	0.61	0.44	0.48	0.021***	0.030 NS	0.088 NS
														0.018	0.025	
Digestibility coefficients:																
gross energy (apparent)	2A	0.97	0.94	0.95	0.97	0.96	0.96	0.96	0.95	0.92	0.95	0.92	0.92	0.009	0.013	
	2B	0.95	0.94	0.96	0.94	0.95	0.95	0.93	0.93	0.93	0.95	0.92	0.94	0.008**	0.011 NS	0.014 NS
														0.006	0.009	
nitrogen (apparent)	2A	0.80	0.67	0.69	0.94	0.94	0.94	0.96	0.96	0.93	0.95	0.94	0.95	0.008	0.012	
	2B	0.70	0.69	0.77	0.90	0.92	0.92	0.93	0.93	0.93	0.94	0.94	0.95	0.007*	0.010* treatment	0.050 NS
														0.006	0.008 1-2-2 only	
nitrogen (true)	2A	1.11	0.94	0.96	1.00	1.00	1.00	0.99	0.99	0.97	0.98	0.96	0.97	0.008	0.012	
	2B	0.99	0.97	1.05	0.96	0.98	0.98	0.96	0.95	0.97	0.97	0.96	0.97	0.007*	0.010* treatment	0.048 NS
														0.006	0.008 1-2-2 only	

[1] 1 pig removed after balance period 1 due to chronic bloat
[2] 1 pig removed during balance period 2A for medication
[3] 1 pig dislodged urine bucket: no urine collection for balance period 2A

[4] n=8 (treatments 2-3-3 and 1-4-4)
[5] n=8 vs 16
[6] n=16 (treatments 1-2-2, 1-2-1, 1-3-3, 1-3-1)
[7] n=4 (treatments 2-3-3 and 1-4-4)
[8] n=4 vs 8
[9] n=8 (treatments 1-2-2, 1-2-1, 1-3-3, 1-3-1)

APPENDIX 3.3: Nitrogen balance and digestibility coefficients in balance periods 3A (3 days) and 3B (7 days) for pigs remaining at the dietary nitrogen intake given during balance periods 2A and 2B (diet controls are provided for comparison)

		Diet No.:							SE difference between:		
		2			*3*		*4*				
	Balance period	2-2-*2*	1-2-*2*	3-3-*3*	1-3-*3*	2-3-*3*	4-4-*4*	1-4-*4*	(i) diets	(ii) balance periods 3A and 3B	(iii) treatments within diets for balance period 3B
No. of pigs	3A	*4*	4	*4*	3†	4	*4*	4			
	3B	*4*	4	*4*	3†	4	*4*	4			
Nitrogen balance (g day^{-1})	3A	*17.43*	17.74	*19.63*	24.56	22.20	*30.50*	32.39	1.231***	1.741* treatment 1-3-*3* only rest NS	
	3B	*17.65*	18.90	*20.08*	29.42	21.98	*30.05*	30.20			3.102* treatment 1-3-*3* only
Nitrogen retained ÷ nitrogen digested	3A	*0.64*	0.63	*0.34*	0.44	0.39	*0.35*	0.36	0.025***	0.035 NS	
	3B	*0.62*	0.66	*0.36*	0.51	0.39	*0.34*	0.35			0.072 NS
Biological value	3A	*0.80*	0.78	*0.43*	0.53	0.48	*0.41*	0.42	0.023***	0.032 NS	
	3B	*0.78*	0.81	*0.44*	0.60	0.48	*0.40*	0.41			0.078 NS
Digestibility coefficients:											
gross energy (apparent)	3A	*0.93*	0.95	*0.95*	0.93	0.95	*0.92*	0.93	0.006*** diet 4 only	0.009 NS	
	3B	*0.95*	0.92	*0.94*	0.94	0.94	*0.91*	0.90			0.014 NS
nitrogen (apparent)	3A	*0.89*	0.92	*0.94*	0.91	0.95	*0.93*	0.94	0.007*	0.010 NS	
	3B	*0.91*	0.92	*0.94*	0.93	0.93	*0.93*	0.93			0.061 NS
nitrogen (true)	3A	*0.95*	0.98	*0.97*	0.96	0.98	*0.95*	0.96	0.007**	0.010 NS	
	3B	*0.97*	0.98	*0.97*	0.95	0.97	*0.95*	0.95			0.061 NS

† 1 pig removed after balance period 2B due to leg weakness

APPENDIX. 3.4: Nitrogen balance and digestibility coefficients in balance periods 3A (3 days) and 3B (7 days) for pigs given a change of dietary nitrogen intake from the end of balance period 2B (diet controls provided for comparison)

	Balance period	Diet No. 1			SE of difference between: (i) balance periods 3A and 3B	SE of difference between: (ii) treatments within balance period 3B	Diet No.: 2		Diet No.: 3		SE of difference between: (i) diets	SE of difference between: (ii) balance periods 3A and 3B	SE of difference between: (iii) treatments in diet balance period 3B
		1-1-*1*	1-2-*1*	1-3-*1*			2-2-*2*	2-1-*2*	3-3-*3*	3-1-*3*			
No. of pigs	3A	*3*†	4	4			*4*	4	*4*	4			
	3B	*3*†	4	4			*4*	4	*4*	4			
Nitrogen retention ($g\ day^{-1}$)	3A	*-0.45*	0.78	-0.85	1.112 NS		*19.63*	20.71	*30.50*	32.45	1.338***	1.892* treatment 3-1-*3* only	
	3B	*0.75*	1.42	1.17		3.102 NS	*20.08*	17.77	*30.05*	25.64			3.102 NS
Nitrogen retained ÷ nitrogen digested	3A	*-0.16*	0.13	-0.14	0.337 NS		*0.64*	0.70	*0.35*	0.57	0.024***	0.034* treatment 3-1-*3* only	
	3B	*0.18*	0.25	0.25		0.072 NS	*0.62*	0.65	*0.34*	0.46			0.072 NS
Biological value	3A	*0.83*	0.95	0.87	0.160 NS		*0.80*	0.85	*0.41*	0.65	0.024***	0.034* treatment 3-1-*3* only	
	3B	*1.05*	1.07	1.04		0.078 NS	*0.78*	0.81	*0.40*	0.55			0.078 NS
Digestibility coefficients:													
gross energy (apparent)	3A	*0.95*	0.95	0.93	0.014 NS		*0.93*	0.95	*0.92*	0.93	0.011 NS	0.015 NS	
	3B	*0.94*	0.95	0.96		0.014	*0.95*	0.94	*0.91*	0.92			0.014 NS
nitrogen (apparent)	3A	*0.67*	0.73	0.60	0.076* treatment 1-3-*1* only		*0.89*	0.94	*0.93*	0.94	0.012 NS	0.016* treatment 2-1-*2* only	
	3B	*0.69*	0.73	0.76		0.061 NS	*0.91*	0.89	*0.93*	0.92			0.061 NS
nitrogen (true)	3A	*0.95*	1.02	0.88	0.076 NS		*0.95*	1.01	*0.95*	0.97	0.012 NS	0.016* treatment 2-1-*2* only	
	3B	*0.99*	1.00	1.05		0.061 NS	*0.97*	0.95	*0.95*	0.95			0.061 NS

† 1 pig removed after balance period 1 due to chronic bloat